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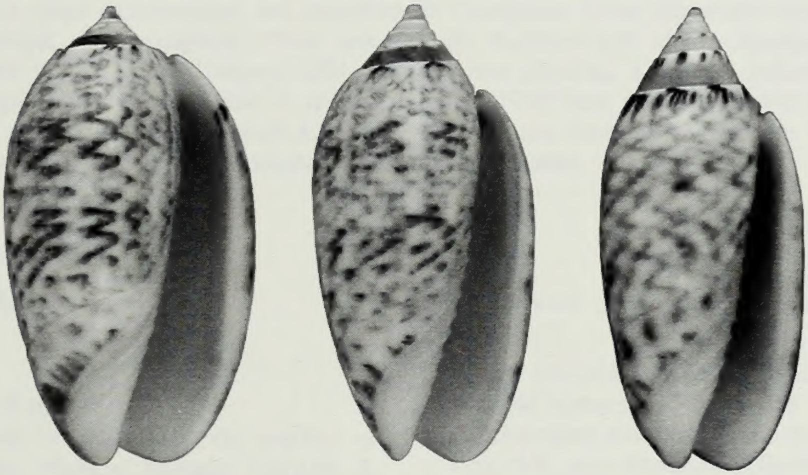
28



A puzzle of highly multiform species: ***Oliva fulgurator*** Röding, 1798) and related American taxa

Bernard TURSCH
Dietmar GREIFENEDER
Dominique HUART

A puzzle of highly multiform species: *Oliva fulgurator* (Röding, 1798) and related American taxa [1]

Bernard TURSCH, Dietmar GREIFENEDER [2] and Dominique HUART.

Laboratoire de Bio-Ecologie, Faculté des Sciences, Université Libre de Bruxelles,
50 av. F.D. Roosevelt, 1050 Brussels, Belgium.

[1]. This is paper n° 28 in the series *Studies on Olividae*.
[2]. Research associate.

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ABSTRACT. The taxonomic status of the members of the Western Atlantic "*Oliva fulgurator-reticularis* complex", the Eastern Pacific "*Oliva spicata* complex" and of some related taxa is reviewed. *O. foxi* Stingley, 1984, *O. fulgurator* (Röding, 1798), *O. polpasta* Duclos, 1833, *O. scripta* Lamarck, 1811 and *O. spicata* (Röding, 1798) are shown to be distinct species. *O. spicata deynzerae* Petuch & Sargent, 1986 is a distinct subspecies. The available type material of many synonymous taxa has been studied and illustrated.

RÉSUMÉ. Le statut taxonomique des membres du "complexe *Oliva fulgurator-reticularis*" de l'Atlantique-Ouest, du "complexe *Oliva spicata*" du Pacifique-Est et de quelques espèces apparentées est revu. *O. foxi* Stingley, 1984, *O. fulgurator* (Röding, 1798), *O. polpasta* Duclos, 1833, *O. scripta* Lamarck, 1811 and *O. spicata* (Röding, 1798) sont démontrées être des espèces distinctes. *O. spicata deynzerae* Petuch & Sargent, 1986 est une sous-espèce distincte. Le matériel type accessible de nombreux taxa synonymes a été étudié et illustré.

1. INTRODUCTION

1.1. The problem

1.1.1. The number of species

Authors differ widely in opinion on the number of *Oliva* species in the Western Atlantic. ZEIGLER & PORRECA (1969) as well as ABBOTT (1974) admit the existence of four species [*Oliva fulgurator* (Röding, 1798), *O. reticularis* Lamarck, 1811, *O. sayana* Ravenel, 1834 and *O. scripta*, Lamarck, 1811]. PETUCH & SARGENT (1986) recognise no less than twenty-one species and ten subspecies.

Many Western Atlantic taxa share common characteristics and appear to be closely related, forming the "*O. reticularis* complex" of TURSCH & HUART (1990) (this shall here be called the "*O. fulgurator-reticularis* complex", for reasons that will become apparent in § 5.1). The numerous, controversial taxa erected for the members of this group are the elements of an old and intricate nomenclatural puzzle, possibly the best example of the notorious taxonomic chaos prevailing in the genus *Oliva*. With the exception of the new species described by PETUCH & SARGENT (1986) and by PETUCH (1987,1988,1990), not hitherto revised, nearly every Caribbean taxon of the complex has already been synonymised (this will be seen in the section Systematics). Only *O. fulgurator* and *O. reticularis* were generally considered to be distinct species. The existence, the nature and the difficulty of the problem raised by the "*O. fulgurator-reticularis* complex" were already clearly grasped well over a century ago:

> "*Oliva reticularis* is, without question, the most variable species in the genus and we warn conchologists that one should have access to a very rich, very abundant collection in order to understand the unions [of taxa] that we are suggesting . . . Let us repeat that such a work requires a considerable collection as well as extreme tenacity".
>
> DUCROS DE SAINT GERMAIN (1857: 53)
> *(translation ours)*

The subsequent naming of many vague and ill-defined forms only added to the confusion. The difficulties encountered in matching shells with names are familiar to every student of Caribbean *Oliva*.

In the Eastern Pacific, ZEIGLER and PORRECA (1969) recognise nine species, while PETUCH & SARGENT (1986) list twenty-one species (and six subspecies). The Eastern Pacific *Oliva* fauna is much richer in species than its Western Atlantic counterpart. It contains a few very distinct species [*O. porphyria* (L., 1758), *O. peruviana* Lamarck, 1811, *O. splendidula* Sowerby, 1825, *O. incrassata* (Lightfoot in Solander, 1786), *O. julieta* Duclos, 1840, *O. kaleontina* Duclos, 1835, *O. undatella* Lamarck, 1811, etc.) which are outstanding in aspect and pose no serious identification problem.

In addition, there is a large group of obviously cognate nominal taxa [the "*O. spicata* complex" based upon *O. spicata* (Röding, 1798), see Tursch & Huart 1990]. This poses much the same problems as its Western Atlantic counterpart, the "*O. fulgurator-reticularis* complex".

1.1.2. The distribution of species

The geographical distribution of many named taxa in both the "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" is poorly known. The limits of their variation are indeed so imprecise that correct identification is often possible only for material from type localities.

Further taxonomic complications arise because several cognate *Oliva* taxa of the two faunas (especially in the "*O. spicata* complex" and in the "*O. fulgurator-reticularis* complex") are quite similar in appearance. Early locality data are often questionable, and in several instances (see examples in Table 1) authors have considered a same taxon to have an Atlantic or a Pacific distribution.

Furthermore, some taxa such as *O. olorinella* Duclos, 1835 (*q.v.*) have been erected upon a mixture of Atlantic and Pacific shells.

1.1.3. Previous quantitative results.

Using morphometric analysis, Tursch & Huart (1990) demonstrated that the Atlantic *Oliva* specimens fall into four objective groups. One of these groups is the West African *O. flammulata* Lamarck, 1811. The three others live in the Western Atlantic: *O. scripta* Lamarck, 1811, *O. sayana* Ravenel, 1834 and a highly variable group then called the "*O. reticularis* complex" (now the "*O. fulgurator-reticularis* complex"). None of these groups could be split into smaller, objective units, although the complex contains very dissimilar populations. The only possible candidate for segregation was *O. oblonga* Marrat, 1870, of which only a small sample was available to us at the time, so that no definite conclusion could be drawn.

Most Eastern Pacific specimens were easily separated into the objective groups *O. porphyria*, *O. splendidula*, *O. kaleontina*, *O. undatella*, *O. polpasta* Duclos,1833 and a large, highly variable group called the "*O. spicata* complex". Further analysis tentatively separated only a sample of *O. polpasta* from a small allopatric sample of *O. kerstitchi* da Motta, 1985. The specific status of the latter was considered to be only a working hypothesis, awaiting further confirmation.

taxon	Eastern Pacific distribution for	Atlantic distribution for
O. brunnea Marrat, 1870	Burch & Burch (1960), Wagner & Abbott (1978) (as a synonym of *O. spicata*)	Petuch & Sargent (1986) (as a subspecies of *O. jamaicensis*)
O. graphica Marrat, 1870	Burch & Burch (1960) (as a synonym of *O. spicata*) Wagner & Abbott(1978) (as a synonym of *O. scripta*)	Zeigler & Porreca (1969), Keen (1971) (as a synonym of *O. julieta*) Petuch & Sargent (1986) (as a full species)
O. oblonga Marrat, 1870	Burch & Burch (1960), Keen (1971), Wagner & Abbott (1978) (as a synonym of *O. spicata*)	Petuch & Sargent (1986), Petuch (1987) (as a form of *O. tisiphona*)
O. oriola ; Duclos (not Lamarck, 1811), 1835.	Burch & Burch (1960), Zeigler & Porreca (1969), Keen (1971) (as a synonym of *O. spicata*)	Wagner & Abbott (1978) (as a synonym of *O. reticularis, pars*)
O. oniska Duclos, 1845	Wagner & Abbott (1978) (as a synonym of *O. fulgurator*) Petuch & Sargent (1986) (as a subspecies of *O. tisiphona*)	Zeigler & Porreca (1969) (as a form of *O. spicata*)
O. porcea Marrat, 1870	Wagner & Abbott(1978) (as a synonym of *O. scripta*)	Burch & Burch (1960) (as a synonym of *O. spicata*) Zeigler & Porreca (1969), Keen (1971) (as a synonym of *O. julieta*)

Table 1. Some examples of divergent geographical attributions.

It was stressed that nearly all the many controversial taxa erected for American species appear:

1/ to have a restricted geographical distribution.

2/ to belong either to the "*O. fulgurator-reticularis* complex" or to the "*O. spicata* complex" (see TURSCH & HUART 1990).

1.2. Aim.

The present paper is the continuation and the extension of the exploratory quantitative survey of living American *Oliva* species by TURSCH & HUART (1990). In that preliminary study, some species were not represented; other required larger samples and nomenclatural problems were not treated in any detail.

The causes of the discrepancy of opinions in the "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" will be analysed and discussed. A critical review of the type material will now be presented.

The very distinct species *O. porphyria, O. peruviana, O. splendidula, O. incrassata, O. julieta, O. kaleontina, O. undatella* will be mentioned in the present paper only as references for the delimitation of the "*O. spicata* complex". The West African species *O. flammulata* will also be considered for comparison because it is the type species of the genus *Strephona* Mörch, 1852, in which many American taxa have been placed (for reasons not clear to us). The taxa *O. schepmani* Weissbord, 1962 [most probably a form of *O. fulgurator* (Röding, 1798)], *O. davisae* Durham, 1950 (most probably a form of *O. polpasta* Duclos, 1833) and *O. callosa* Li, 1930 (a subjective junior synonym of *O. polpasta* Duclos, 1833) all based upon fossil material, will not be examined here.

2. MATERIAL EXAMINED

2.1. Specimens.

372 specimens, from many localities, have been added to the 419 specimens measured in detail and listed in TURSCH & HUART (1990). In addition to the material measured, several thousand specimens, from a large number of localities, have been examined in public and private collections. Broad localities for specimens of the "*O. fulgurator-reticularis* complex", the main object of this study are shown on the map of Fig. 1. The complete list of the examined material would take many pages and (contrary to our habit) we have preferred to list only the type material. 35 measurements (17 used in this paper) have been determined on each intact specimen measured, so this work rests upon a databank of well over twenty thousand high-precision measurements (see section 3.1), accumulated over many years.

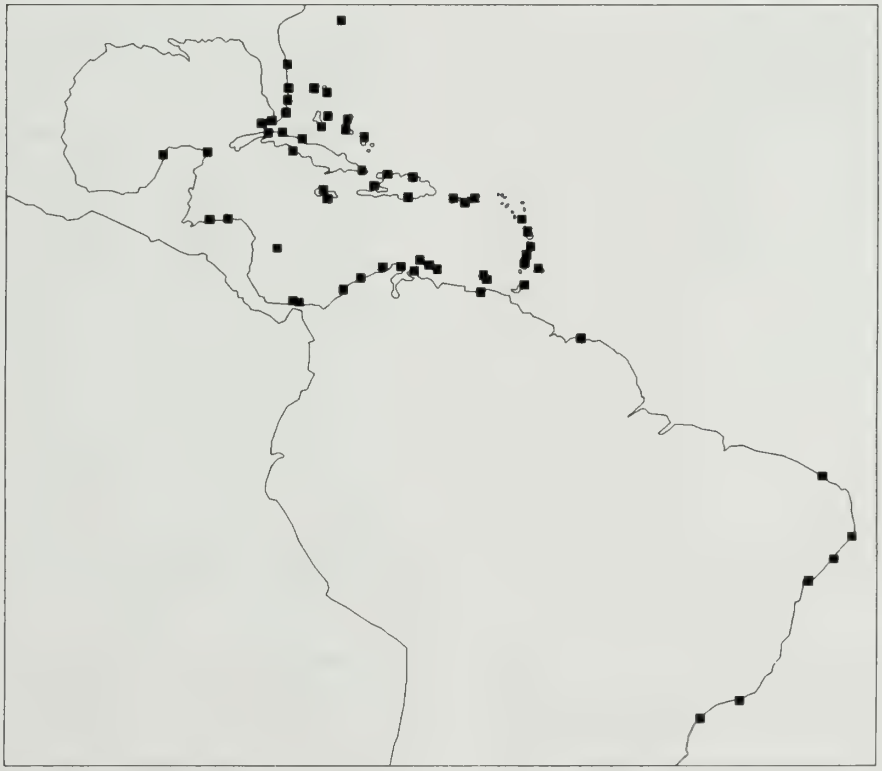

Fig. 1. The "*O. fulgurator-reticularis* complex". Localities of material examined. Localities in close vicinity (less than 20 miles) not separated.

2.2. Abbreviations:

AMS: Australian Museum, Sydney.

AMNH: American Museum of Natural History, New York.

ANSP: Academy of Natural Sciences, Philadelphia.

BM(NH): The Natural History Museum, London.

MCM: Merseyside County Museum, Liverpool.

MCZ:Museum of Comparative Zoology, Harvard University.

MNHN: Muséum National d'Histoire Naturelle, Paris.

MHNG: Muséum d'Histoire Naturelle, Genève.

USNM: National Museum of Natural History (Smithsonian Institution), Washington.

SBMNH: Santa Barbara Museum of Natural History.

SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt.

2.3. Type material examined.

Oliva foxi Stingley, 1984.

Oliva foxi Stingley, 1984. Holotype ANSP 358356 (H: 36.98 mm, D: 14.82 mm) (see Pl. 4, fig. 1). One paratype ANSP 358357 (H: 37.60 mm, D: 15.17 mm) (see Pl. 4, fig. 2). One paratype AMNH 264800 (H: 34.9 mm, D: 14.1 mm) (see Pl. 4, fig. 3). One paratype AMS C.170890 (H: 33.35 mm; D: 13.36 mm) (see Pl. 4, fig. 4).

Oliva fulgurator (Röding, 1798).

Oliva olorinella Duclos, 1835. Eight heterogeneous syntypes at MNHN. One syntype (H: 28.7 mm; D: 12.1 mm) illustrated Pl. 9, fig. 2.

Oliva obesina Duclos, 1840. Figured syntype (H: 44.0; D: 26.3 mm) (see Pl. 6, fig. 1), and 2 syntypes at MNHN.

O. timoria Duclos, 1840 (*pars*). Figured syntype (out of 3) (H: 62.0 mm; D: 33.1 mm), MNHN. (see Pl. 7, fig. 1).

Oliva aldinia Duclos, 1845. Figured syntype (H: 55.6 mm, D: 30.3 mm), (see Pl. 6, fig. 2) + 3 syntypes at MNHN.

Oliva broderipi Ducros de St. Germain, 1857. Holotype at MNHN (H: 27.8 mm; D: 13.4 mm) (see Pl. 7, fig. 3).

Oliva jamaicensis Marrat, 1867. Holotype at MCM (H: 37.7 mm, D: 18.4 mm) (see Pl. 6, fig. 6).

Oliva oblonga Marrat, 1867. Holotype at MCM (H: 63.2 mm, D: 29.2 mm) (see Pl. 6, fig. 7).

Oliva bewleyi Marrat, 1870. Holotype at MCM (H: 41.8, D: 18.1 mm) (see Pl. 7, fig. 10).

Oliva figura Marrat, 1870. Holotype at MCM (H: 41.2 mm, D: 18.1 mm) (see Pl. 8, fig. 3).

Oliva formosa Marrat, 1870. Holotype at MCM (H: 45.23 mm; D: 19.52 mm) (see Pl. 9, fig. 6).

Oliva graphica Marrat, 1870. Holotype at MCM (H: 44.6 mm, D: 22.2 mm) (see Pl. 6, fig. 4).

Oliva porcea Marrat, 1870. Holotype at MCM (H: 42 mm, D: 20.8 mm) (see Pl. 6, fig. 3).

Oliva sowerbyi Marrat, 1870. Syntype (out of 2) at MCM (H:32.2 mm; D:15.0 mm). This taxon is not related to *O. fulgurator* (see Systematics).

Oliva bullata Marrat, 1871. Holotype at MCM (H: 60.83 mm; D: 26.21 mm) (see Pl. 9, fig. 3).

Oliva mercatoria Marrat, 1871. Two syntypes at MCM (H: 41.0 mm, D: 19.5 mm and H: 44.2 mm, D: 20.5 mm) (see Pl. 6, fig. 9).

Oliva nivosa Marrat, 1871. Holotype (H: 49.2 mm, D: 22.0 mm) (see Pl. 7, fig. 9) and one possible paratype at MCM.

Oliva reclusa Marrat, 1871. Holotype at MCM (H: 43.2 mm, D: 18.1 mm) (see Pl. 9, fig. 7).

Oliva circinata Marrat, 1871. Holotype at MCM (H: 55.4, D: 23.4 mm) (see Pl. 9, fig. 8), with 4 possible paratypes. One probable paratype (as stated on an additional label written by N. McMillan in 1978) ANSP 15940 (H: 47.02 mm, D: 19.64 mm).

Oliva bifasciata Küster in Weinkauff, 1878. Figured specimen SMF 9353 (H: 61.39 mm, D: 26.73 mm) (see Pl. 8, fig. 4).

Oliva cribraria Marrat, 1883? Holotype (H: 48.22 mm; D: 22.12 mm) at MCM (see Pl. 9, fig. 10).

Oliva reticularis bollingi Clench, 1934. Holotype MCZ 76656 (H: 61.95 mm, D: 28.52 mm) (see Pl. 7, fig. 8).

Oliva reticularis greenwayae Clench, 1937. Holotype MCZ 115455 (H: 59.65 mm, D: 25.18 mm) (see Pl. 8, fig. 5).

Oliva pattersoni Clench, 1945. Holotype MCZ 151166 (H: 62.57 mm, D: 28.29 mm) (see Pl. 8, fig. 6).

Oliva drangai Schwengel, 1951. Holotype ANSP 247107 (H: 40.47 mm, D: 18.62 mm) (see Pl. 7, fig. 7). Paratype ANSP 247093 (H: 18.56 mm, D: 8.46 mm).

Oliva antillensis Petuch & Sargent, 1986. Holotype USNM 841425 (H: 28.05 mm; D: 11.47 mm) (see Pl. 9, fig. 1).

Oliva ionopsis Berry, 1969. Holotype SMBNH 34656 (H: 30.54 mm; D: 13.76 mm) (see Pl. 11, fig. 10) and seven paratypes SMBNH 34657.

Oliva bahamasensis Petuch & Sargent, 1986. Holotype USNM 841426 (H: 44.58 mm; D: 20.62 mm) (see Pl. 8, fig. 10).

Oliva barbadensis Petuch & Sargent, 1986. Holotype USNM 841427 (H: 47.05 mm; D: 20.32 mm) (see Pl. 9, fig. 4).

Oliva bifasciata jenseni Petuch & Sargent, 1986. Holotype USNM 859302 (changed from USNM 841453, R. Germon *in litt.*) (H: 50.30 mm; D: 24.12 mm) (see Pl. 7, fig. 6).

Oliva finlayi Petuch & Sargent, 1986. Holotype USNM 841432 (H: 39.98 mm; D: 18.71 mm) (see PL. 8, FIG. 8).

Oliva goajira Petuch & Sargent, 1986. .Holotype USNM 841433 (H: 36.79 mm; D: 15.49 mm) (see PL. 8, FIG. 2).

Oliva jamaicensis zombia Petuch & Sargent, 1986. Holotype USNM 841454 (H: 23.87 mm; D: 12.61 mm) (see PL. 7, FIG. 2).

Oliva magdae Petuch & Sargent, 1986. Holotype USNM 841441 (H: 37.57 mm; D: 18.62 mm) (see PL. 6, FIG. 8).

Oliva maya Petuch & Sargent, 1986. Holotype USNM 859301 (changed from USNM 841453, R. GERMON *in litt.*) (H: 57.81 mm: D: 24.97 mm) (see PL. 8, FIG. 1).

Oliva bifasciata sunderlandi Petuch, 1987. Holotype USNM 859904 (H: 22.02 mm; D: 9.56 mm) (see PL. 9, FIG. 5).

Oliva circinata tostesi Petuch, 1987. Holotype USNM 859865 (H: 46.20 mm; D: 21.37 mm) (not H: 41 mm as in description) (see PL. 9, FIG. 9).

Oliva sargenti Petuch, 1987. Holotype USNM 859864 (H: 28.60 mm; D: 14.03 mm) (see PL. 7, FIG. 5).

Oliva contoyensis Petuch, 1988. Holotype USNM 859945 (H: 36.71 mm; D: 18.42 mm) (see PL. 7, FIG. 4).

Oliva ernesti Petuch, 1990. Holotype USNM 860535 (H: 33.66 mm, D: 15.45 mm) (not H: 38 mm, as in description) (see PL. 8, FIG. 7).

Oliva polpasta Duclos, 1833.

Oliva polpasta Duclos, 1833. Six syntypes at MNHN. Figured syntype (H: 40.1 mm; D: 21.0 mm) (see PL. 4, FIG. 6).

Oliva truncata Marrat, 1867. Holotype at MCM (H: 37 mm, D: 18 mm) (see PL. 4, FIG. 7).

Oliva kerstitchi da Motta, 1985. Holotype MHNG 984.631 (H: 24.5 mm, D: 11.2 mm) (see PL. 4, FIG. 8).

Oliva olssoni Petuch & Sargent, 1986. Holotype USNM 841444 (H: 35.03 mm; D: 19.57 mm) (see PL. 4, FIG. 9).

Oliva sayana Ravenel, 1834.

Oliva circinata var. *citrina* Johnson, 1911. Paratype MCZ 6267 (H: 60.51 mm, D: 23.56 mm) (see PL.5, FIG. 4).

Oliva sayana sarasotensis Petuch & Sargent, 1986. Holotype USNM 841450 (H: 40.60 mm; D: 17.90 mm) (see PL. 5, FIG. 3).

Oliva sayana texana Petuch & Sargent, 1986. Holotype USNM 841465 (H: 43.60 mm; D: 17.54 mm) (see PL. 5, FIG. 2).

Oliva scripta Lamarck, 1811.

Oliva caribaeensis Dall & Simpson, 1901. Holotype USNM 159672 (H: 31.61 mm; D: 14.93 mm) (see PL. 5, FIG. 6).

Oliva trujilloi Clench, 1938. Holotype MCZ 57240 (H: 40.52 mm, D: 17.95 mm) (see PL. 5, FIG. 7). One paratype AMNH 79010 (H: 34.8, D: 15.5 mm) (see PL. 5, FIG. 8). Five paratypes AMS C.095147 (one H: 39.57 mm; D: 18.59 mm, illustrated PL. 5, FIG. 9).

Oliva (Cariboliva) scripta venezuelana Petuch & Sargent, 1986. Holotype USNM 841451 (H: 44.22 mm; D: 22.02 mm) (see PL. 5, FIG. 10).

Oliva spicata (Röding, 1798).

Oliva oniska Duclos, 1845. Nine syntypes at MNHN. Figured syntype (H: 61.0 mm; D: 26.2 mm) (see PL. 11, FIG. 4).

Oliva pindarina Duclos, 1840. Three syntypes at MNHN. Figured syntype (H: 53.4 mm; D: 27.3 mm) (see PL. 10, FIG. 2).

O. timoria Duclos, 1840 (*pars*). Figured syntype (out of 3) (H: 55.8 mm; D: 39.1 mm), MNHN. (see PL. 10, FIG. 1).

Oliva subangulata Philippi, 1848. One syntype (H: 59.62 mm; D: 26.38 mm) out of 2, BM(NH) 1924.1.5.98-99. (see PL. 11, FIG. 6).

Oliva cumingii Reeve, 1850. Three syntypes BM(NH) 1987008, (one H: 48.4 mm; D: 24.2 mm) (see PL. 11, FIG. 1).

Oliva ligneola Reeve, 1850. Two heterogeneous syntypes BM(NH) 1892.9.24.4-5. One (H: 21.36 mm; D: 10.67 mm) is *O. tigrina fallax* Johnson 1911, the other (H: 25.60 mm; D: 13.09 mm) (see PL. 10, FIG. 3) is a bleached *O. spicata* (Röding), 1798.

Oliva intertincta Carpenter, 1857. Two syntypes USNM 716187 (largest: H: 19.68 mm; D: 9.70 mm, see PL. 11, FIG. 9). 3 additional syntypes in BM(NH), Carpenter collection, tablet 2121.

Oliva violacea Marrat, 1867. Holotype at MCM (H: 39.3 mm, D: 17.3 mm) (see PL. 11, FIG. 8).

Oliva brunnea Marrat, 1870. Holotype at MCM (H: 34,0 mm, D: 16.1 mm) (see PL. 11, FIG. 3).

Oliva punctata Marrat, 1870. One of two syntypes (H: 35.35 mm; D: 17.24 mm) at MCM (see PL. 10, FIG. 4).

Oliva fuscata Marrat, 1870. Three syntypes at MCM, one of which (H: 42.66 mm; D: 20.30 mm) is figured PL. 11, FIG. 2 and another (H: 39.76 mm; D: 18.62 mm) PL. 11, FIG. 7.

Oliva spicata var. *hemphilli* Ford in Johnson, 1911. Five syntypes ANSP 111697. One (H: 54.05 mm, D: 23.38 mm) is figured PL. 10, FIG. 8.

Oliva spicata var. *perfecta* Johnson, 1911. Three syntypes ANSP 111729. One (H: 59.06 mm, D: 25.73 mm) is figured PL. 11, FIG. 5.

Oliva rejecta Burch & Burch, 1962. One paratype USNM 667317 (H: 37.24 mm; D: 16.01 mm) (see PL. 10, FIG. 10). One paratype at MNHN (H: 31.3, D: 13.6 mm) (see PL. 10, FIG. 9).

Oliva (Strephona) radix Petuch & Sargent, 1986. Holotype USNM 841446 (H: 36.62mm; D: 22.51 mm) (see PL. 10, FIG. 6).

Oliva subangulata corteziana Petuch & Sargent, 1986. Holotype USNM 841457 (H: 32.33 mm; D: 16.21 mm) (see PL. 10, FIG. 7).

Oliva spicata deynzerae Petuch & Sargent, 1986.

Oliva (Strephona) spicata deynzerae Petuch & Sargent, 1986. Holotype USNM 841452 (H: 53.19 mm; D: 21.95 mm) (see PL. 4, FIG. 5).

3. METHODS

3.1. Measurements.

The protoconch measurements NW, SPRO, MPRO, LPRO, RES5, PAT17, PAT18 and the teleoconch measurements PNW, H, L, LW, D, R, X, F, FG and SUT that are utilized in this work have been defined in detail by TURSCH & GERMAIN (1985, 1986, 1987). They have been repeatedly tested and demonstrated to be operational in the genus *Oliva* (see TURSCH, GERMAIN & GREIFENEDER 1986a, 1986b; TURSCH & HUART 1988; 1990; TURSCH 1988, 1994; TURSCH & GREIFENEDER 1989a, 1989b; TURSCH, MISSA & BOUILLON 1992).

For a quick reminder, these measurements are sketched in Fig. 2. Two important measurements do not appear on this figure. NW is the number of nuclear whorls and PNW is the number of postnuclear whorls. Both are measured to 0.05 whorl. The way in which *Oliva* shell measurements are best used is discussed in TURSCH & GREIFENEDER (1996).

3.2. Analysis methods.

These are essentially the same as in TURSCH, MISSA & BOUILLON (1992) and TURSCH & GREIFENEDER (1996). Each specimen can be represented by a point in the attribute hyperspace, *i.e.*, a space having as many dimensions as there are variables (attributes) under consideration. Any phenon will thus appear as a cloud of points in the attribute hyperspace, the dimensions of the cloud reflecting variability.

Separations (voids between clouds of points) in hyperspace cannot be visualized directly. These voids can be detected by special techniques of space reduction, such as Principal Component Analysis (PCA) or Factorial Discriminant Analysis (FDA). In favourable situations, however, only two of the many variables can be sufficient for evidencing the separation of two or several groups. This can then be represented on bidimensional graphs (scatter diagrams). Such separations constitute conclusive evidence: groups that are separated in two dimensions are necessarily separated in the multidimensional attribute hyperspace. From our experience, patient search for operational characters (the number of possible combination of measurements can be very large) will generally yield a clean-cut bidimensional representation of the separations. The search for such operational characters is greatly helped by preliminary PCA and FDA studies.

Only scatter diagrams will be reported here: they convey all the necessary evidence and are much more heuristic than PCA or FDA graphs. Numerical results will be reported here only when really needed. Reporting, for instance, the very evident differences separating *O. porphyria* from *O. kaleontina* in numerical terms would be quite superfluous. It would consume space and unnecessarily tax the patience of the reader.

Reading graphs containing hundreds of points is very strenuous. We have therefore preferred to represent the distribution of attributes by plain minimum convex polygons.

3.3. Interpretation of data.

As in nearly all taxonomic studies of Mollusks, the morphospecies approach is adopted here. On the one hand it is evident (but often overlooked) that one can never give a real *demonstration* that two objects (in this case, lots of shells) belong to the same morphospecies. In practice, two specimens belong to the same morphospecies if they are linked by an unbroken chain of intermediate specimens (sympatric or not).

On the other hand, one can present convincing arguments that two (or more) samples belong to separate morphospecies. Two morphospecies are distinct if their representative clouds in the attribute hyperspace are separated by a void region: a morphological gap. To prevent taxonomy from becoming a game of chance, only ***full separations*** (with no overlap) will be taken into account in this work. If one cannot bring forwards such arguments, then one has no choice: unseparated samples must be considered as belonging to the same morphospecies (awaiting further, objective arguments to the contrary).

Great care should be exercised in the interpretation of the observed separations (see TURSCH & GREIFENEDER 1996). The general problem of detecting separations is much aggravated in multidimensional hyperspaces (where one can get horribly lost). In the bidimensional graphs used in this work, interpretation is much safer but caution is neverteless required. First, one has to consider the size of the samples. In scatter diagrams, weak separations and separations obtained on small samples (from our experience, $N<6$) might be indicative but must be considered with caution. Small gaps observed between small samples should be interpreted with great prudence. All separations accepted in this work are supported by additional evidence: the observed gaps correspond to discontinuities in the distribution of other characters, unrelated to the nature of the axes of the graph (other metric characters, colour pattern features, distributional data, etc.).

In contrast, observed *overlaps are always significant*, as these overlaps will persist if the size of the sample is increased. Even one single specimen can be legitimately tested by comparison with a large sample. This allows the demonstration of overlaps in the case of type material.

The interpretation of morphometric separations in terms of distinct species is straightforward only for samples that are syntopic (*i.e.*, actually live together, in the same microbiotope). Only in these conditions can morphological gaps be safely interpreted in terms of reproductive barriers.

It has been shown (TURSCH 1994) that *Oliva* species consist of a mosaic of distinct populations, each being quite homogeneous. When a large enough number of such local, conspecific populations are compared, they invariably show considerable character overlap. The species is thus represented by a ***morphological continuum*** in the attribute hyperspace. This is a set in which no population (or groups of populations) can be separated from all the others. Even if two (or more) of the populations forming the continuum can be easily separated from each other, the gap is invariably bridged by another conspecific population (or an unbroken chain of intermediate populations). The boundaries of the morphological continuum are the limits of the phenetic variability of a species.

Completely separable populations belonging to the same *Oliva* species can occur even within very short geographic distances (TURSCH 1994). Separations between pairs of conspecific populations are thus fully expected (see MAYR & ASHLOCK 1991 and FUTUYMA 1986) and do not constitute grounds for specific discrimination. Well on the contrary, observation that very similar *Oliva* phena do never co-occur constitutes a strong indication of their conspecificity (TURSCH 1995).

In the morphospecies approach, specific discrimination can be established only by the separation of sets containing as many different local populations as possible. Even with a small number of specimens, samples including *Oliva* shells from different localities include much more of the total variability of the species. Clear separations of such samples are more probably significant.

Other problems can occur within the population level. Sexual dimorphism can fortunately be neglected in the genus *Oliva*. In contrast, some *Oliva* species have a non-isometric growth (TURSCH 1997) and in such instances, unless adequate precautions are taken, artificial segregation of young and aged individuals can easily occur.

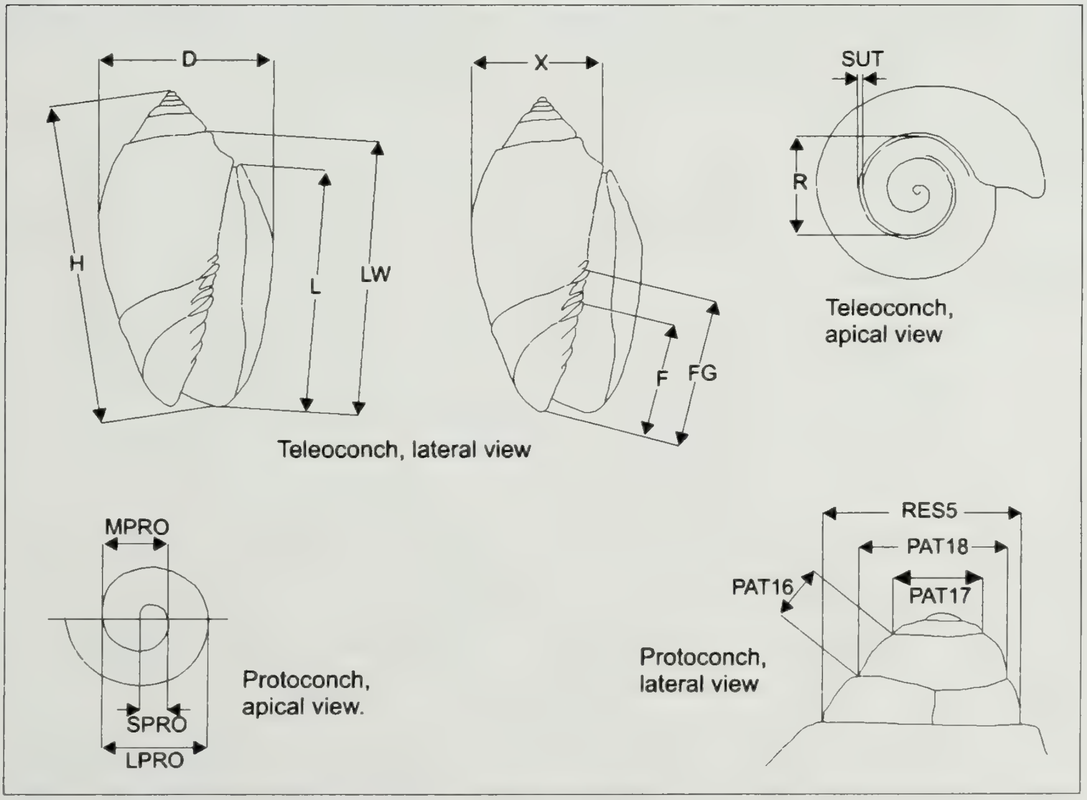

Fig. 2. Sketch of shell measurements used in this work.

In theory, the objective approach advocated here could either increase the number of species (by detecting previously overlooked gaps) or reduce it (by demonstrating previously overlooked overlaps). In practice, it does lead to a sharp diminution of the number of admitted species. This is frequently called *'lumping'* by collectors who 'know' their shells. Please note that *'splitters'* and *'lumpers'* can exist only when taxonomic decisions are a matter of personal opinion. This can certainly be the case at the supraspecific level, where one can disagree on where to 'cut the branches' of a phylogenetic tree. But the species is (or at least should be) the most objective of all taxonomic categories. At the species level, we should not even have the choice between *'splitting'* and *'lumping'*. These two attitudes can, at best, be provisional strategies for handling unsolved cases.

In summary, the method used in this work is very simple. A large number of purposely unidentified specimens are first shown to be separated into distinct morphological groups. By careful selection of characters (using PCA and FDA), the separations of the groups could be demonstrated in bidimensional representations. In spite of all efforts, these groups could not be split any further (even when submitted to PCA and FDA tests on all variables). We consider these groups as separate morphospecies, a conclusion supported by the fact that all additional specimens fall into these clusters. If the type material of other taxa cannot be separated from these groups, synonymy is demonstrated

The species so defined can now be visually identified with a rather high degree of confidence because the distribution of morphometric characters is correlated to the distribution of some (mostly undescribed) visual clues. But these clues could be found only after morphometric analysis. Many 'intuitive species' erected only on other, uncorrelated visual clues are listed in a specially long synonymy (see Index to names).

4. RESULTS AND OBSERVATIONS

4.1. Species delimitation.

The inclusion of many additional specimens in the morphometric analysis did not fundamentally modify the conclusions previously drawn by TURSCH & HUART (1990). For instance, all the Atlantic and Eastern Pacific *Oliva* species are included in the scatter diagram of Fig. 3, where many species are objectively separated in one single operation. *O. foxi* Stingley, 1984 (not considered in TURSCH & HUART 1990) is completely separated from *O. spicata* and *O. polpasta*. The species *O. incrassata*, *O. julieta* and *O. peruviana* (also not considered in TURSCH & HUART 1990) are clearly separated from cognate species and will not be treated here anymore, except for comparison.

All the Atlantic *Oliva* taxa still fall into four objective groups, clearly separated even on one single scatter diagram (see Fig. 4). One of these groups is *O. flammulata* Lamarck, 1811, confined to the West African coast, with a subspecies *O. flammulata dolicha* Locard, 1896 in Cabo Verde (see TURSCH & HUART, 1988). It will not be treated here anymore, except for comparison. The three others live in the warm waters of the Western Atlantic. Two of these objective groups correspond to the species *O. scripta* Lamarck, 1811 and *O. sayana* Ravenel, 1834. These groups are quite homogeneous and could not be split into smaller, objective units.

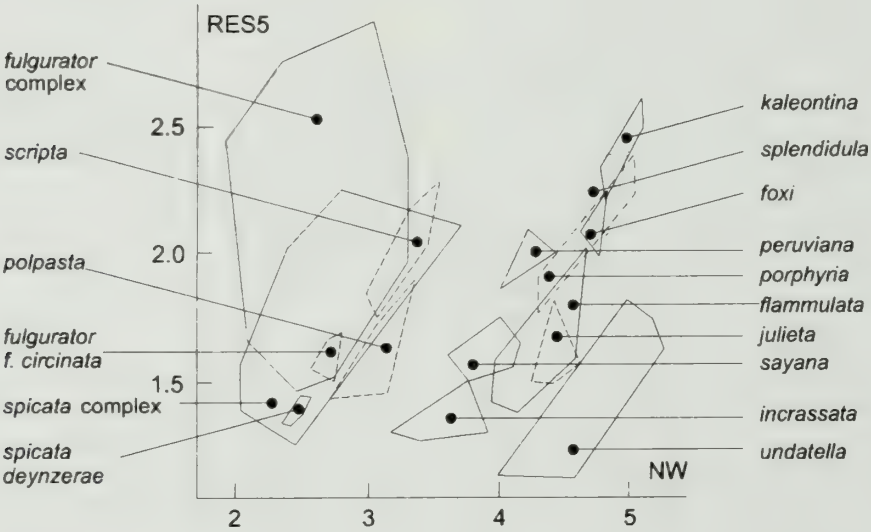

Fig. 3. All Atlantic and Pacific species. Scatter diagram: RES5 *vs.* NW. Minimum convex polygons. Every group is well separated with other variables, with the exception of the "*O. fulgurator* complex" not separated from the "*O. spicata* complex".

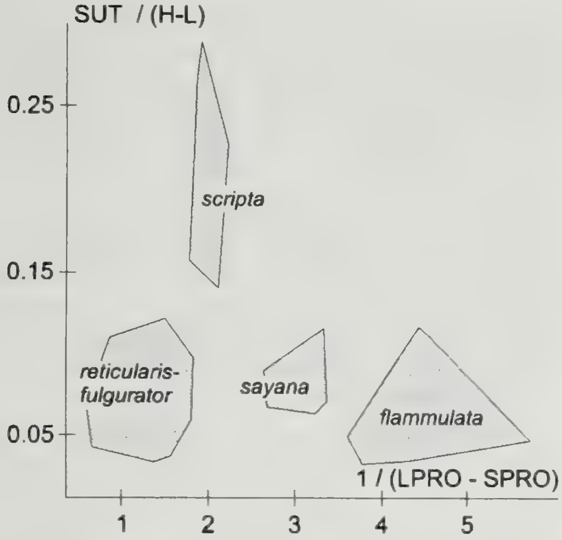

Fig. 4. Separation of Atlantic *Oliva* species. Scatter diagram: SUT/(H-L) *vs.* 1/(LPRO-SPRO). Minimum convex polygons.

The third Western Atlantic group, the "*O. fulgurator-reticularis* complex", has a much higher variability, as attested by the relative dimensions of its representative cloud of points in most dimensions of the attribute hyperspace. Some of the populations that it contains are indeed very dissimilar in aspect. In spite of much effort spent to that end, this "complex" could not be objectively split into smaller units. Inclusion of additional specimens now established that *O. oblonga* Marrat, 1870, formerly thought by us to be a possible candidate for separation (see TURSCH & HUART 1990), does considerably overlap with the complex.

In the Eastern Pacific, all the separations previously observed persisted, with only one exception. A scatter diagram of R/L vs. NW/(LPRO-SPRO) (Fig. 5) clearly separated *O. porphyria* and *O. splendidula* from two large, distinct, but not homogeneous groups

These two unresolved groups (NH) were then analysed in a scatter diagram of PAT18/NW vs. LPRO (Fig. 6) yielding four groups corresponding to *O. kaleontina, O. undatella, O. polpasta* and the "*O. spicata* complex". None of these final groups could be objectively split into smaller units. One result differed from the previous ones: with the inclusion of additional, allopatric specimens, *O. polpasta* Duclos,1833 could not anymore be separated from *O. kerstitchi* da Motta, 1985 [this separation was suggested in Tursch & Huart (1990) as a working hypothesis awaiting further confirmation].

In spite of much effort to that end, no quantitative discrimination of the "*O. fulgurator-reticularis* complex" from the "*O. spicata* complex" could be established, as already observed in TURSCH & HUART (1990). A very large number of separation attempts (including frequency histograms, scatter diagrams, principal factor analysis, discriminant factorial analysis and UPGMA clustering) invariably resulted in considerable overlap between the two groups, as in the example of Fig. 7. There is nothing really new in this observation:

> "The discrimination of... [*O. melchersi* and *O. venulata*] ... from each other and from *O. reticularis* is a matter of extreme difficulty; which Mr. Reeve escapes by uniting them all together."
>
> CARPENTER (1855: 464).

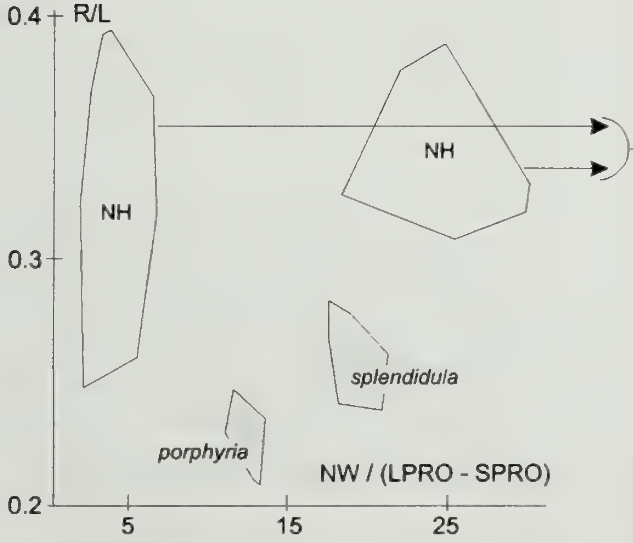

Fig. 5. Separation of Eastern Pacific *Oliva* species. Scatter diagram: R/L vs. NW/(LPRO-SPRO). Minimum convex polygons. The groups marked NH are not homogeneous.

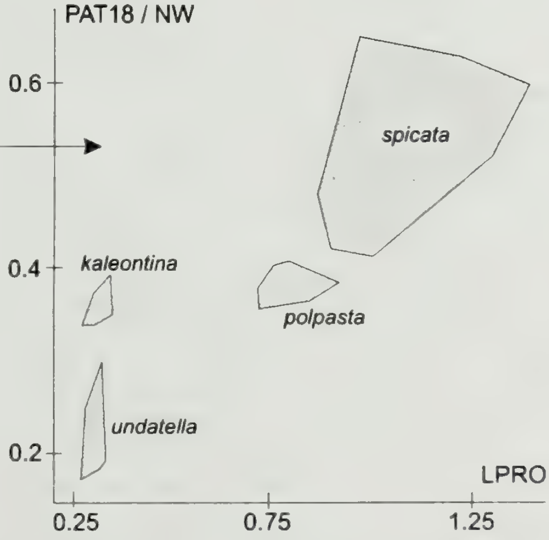

Fig. 6. Separation of Eastern Pacific *Oliva* species. Separations of the groups NH unresolved in Fig. 5. Scatter diagram: PAT18/NW vs. LPRO. Minimum convex polygons.

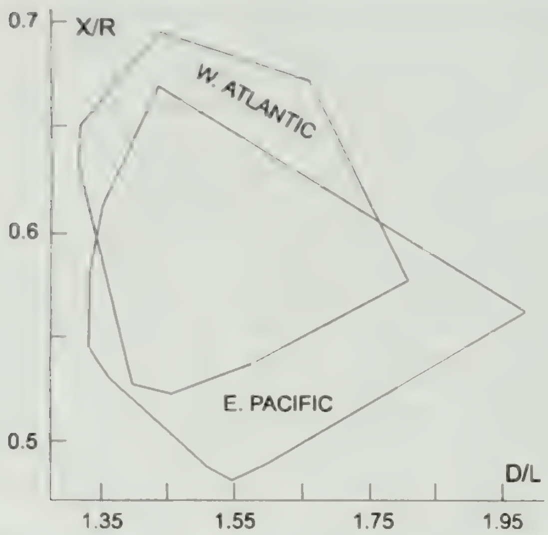

Fig. 7. Attempted separation of the "O. *fulgurator-reticularis* complex" (marked "W. Atlantic") from the "O. *spicata* complex" (marked "E. Pacific"). One example amongst many. Scatter diagram: X/R *vs.* D/L. Minimum convex polygons.

Because of their long-standing disjunct geographical distribution (and only for that reason), this constant overlap does not necessarily mean that the two groups are of the same species (see § 5.4).

Many of the groups defined here above have quite characteristic protoconchs. Examples are given in Fig. 8 and Fig. 9. One will note the exceptionally great variation range of the protoconchs of *O. fulgurator* and *O. spicata*. This variation is way larger than for any of the Indo-Pacific species that we have examined. The ranges of variation of all subsamples form an unbroken continuum (see § 4.4).

Two characteristics of the shell colour pattern confirm the close (and expected) relationship of the Western Atlantic and Eastern Pacific *Oliva* faunas, and set a number of species apart from all others. In the genus *Oliva*, the presence on the shell of a peculiar colour pattern located just under the filament channel is a reliable indication that one is dealing with an American species (for details on the filament channel, see VAN OSSELAER & TURSCH 1994). This repeated pattern consists in bundles of divaricate, fasciculated, fine lines meeting at a central point or a small blotch, right at the sharp exterior edge of the channel (see Fig. 10). It is -as expected- very variable but nevertheless highly recognisable. It will be referred here under as the "*fasciculated pattern*", for short. The presence on the shell of this pattern, quite unique in the genus *Oliva*, is a safe indication that one is dealing with either a Western or an Eastern American species. It is indeed present in all American *Oliva* species, except *O. kaleontina*, *O. peruviana* and *O. undatella* (see Plate 1). It is not clearly present in *O. flammulata* Lam., 1811 (possible intermediates are occasionally met). It is not found in any Indo-Pacific species (with the possible exception of an intermediate pattern found on the Hawaiian, deep water *O. richerti* Kay, 1979 from Hawaii). The presence of this same subchannel pattern in species as different as *O. porphyria* and *O. spicata* could be interpreted as indicating a common, but ancient ancestry.

There is one other shared feature in the colour pattern. Most species of the genus *Oliva* display two more or less diffuse spiral bands of darker colour on the body whorl. It has been shown by GREIFENEDER (1984) that the relative position of these bands in many American *Oliva* species is consistently lower than that observed in their Indo-Pacific congenerics.

Another argument yet could be found in the orientation of the shell microcrystalline layers. The distribution of angular values in both the Western Atlantic and Panamic *Oliva* species has been shown to differ from that of their Indo-Pacific counterparts. This should be interpreted with caution because the phenomenon could possibly be of adaptative nature (TURSCH & MACHBAETE 1995).

4.2. Homogeneous, distinct local populations.

Except for occasional colour variants, the local populations of the members of the "*fulgurator-reticularis* complex" are quite homogeneous in shape and general outline (see DIAZ & PUYANA 1994: 202). Albeit variable (colour polymorphism results in occasional colour variants such as darker or paler individuals) the ground colour of the shell is generally cryptic, matching the substrate, just as for most Indo-Pacific *Oliva* species (see VAN OSSELAER *et al.* 1993). This homogeneity (probably due to the inefficiency of immigration into generally large populations –see § 6.1- and possibly maintained by selection) does restrict even more the intra-population variation.

In contrast, inter-population variation is much greater, considerable differences being often observed between specimens from different localities. This was already clearly perceived by DIAZ & PUYANA (1994: 202), who wrote about *O. bewleyi* Marrat, 1870:

> "Note: this species is very variable in its colour pattern, even within one local population. Variations in the form of the shell (height of the spire, ratio height/width, etc.) are frequent between populations but not so within one same population. Within the abundant material of *O. bewleyi* from different localities of the Colombian and Venezuelan Caribbean examined by us, and applying the criteria of Sargent & Petuch (1986), not less than six different 'species' or 'subspecies' exist in the region..."
>
> (*translation ours*).

That the distribution of most of the populations is quite restricted, is evidenced by the fact that the experienced collector can often guess the origin of a given specimen.

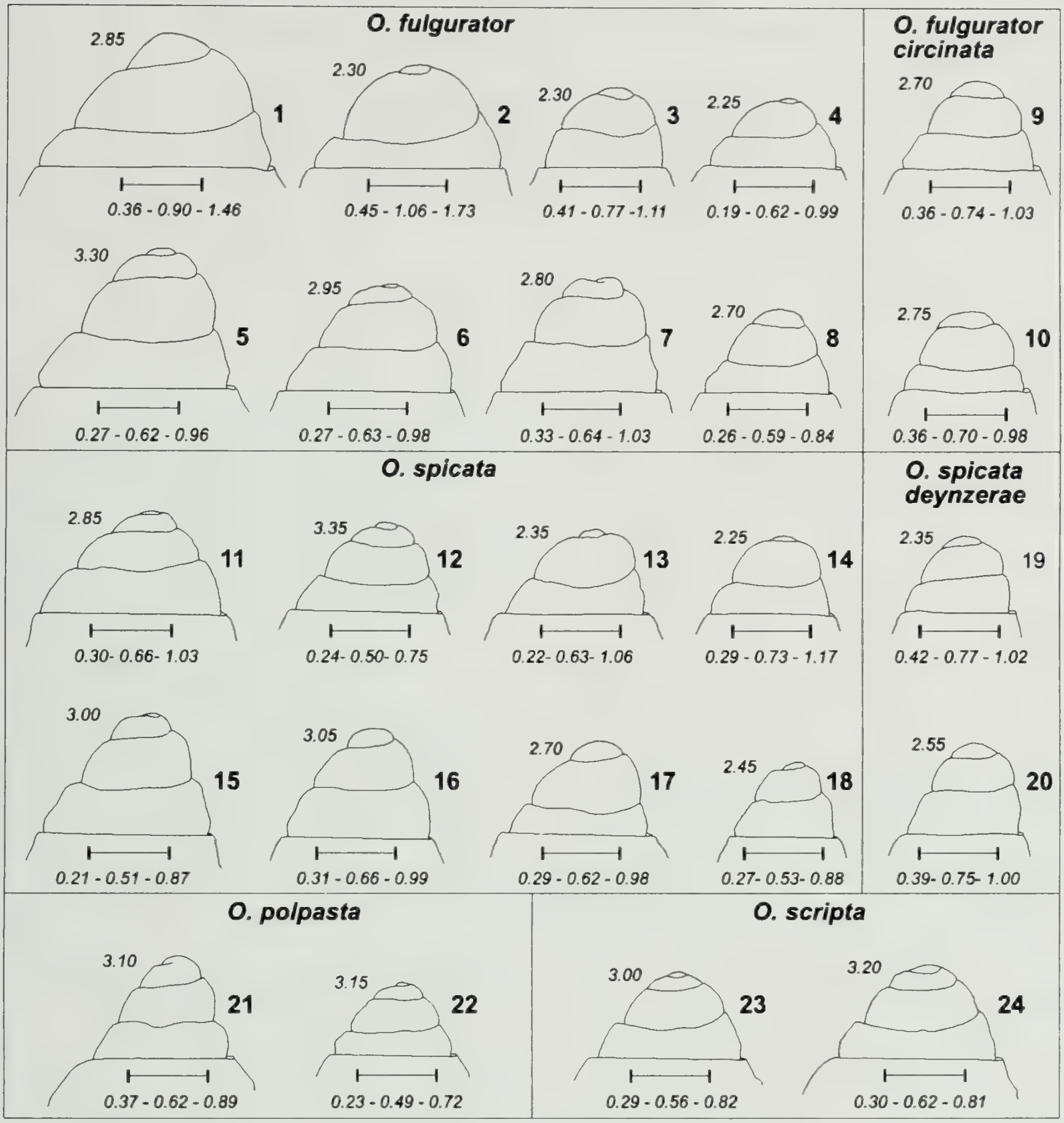

Fig. 8. Protoconchs (Atlantic). Scale bars: 1 mm. Figures to the left of apex: number of nuclear whorls (NW). Figures below scale bar: measurements SPRO, MPRO and LPRO of first protoconch volutions (see Fig. 2).

1-10: ***O. fulgurator*** (Röding, 1798). ***1***: Isla Boracha, Venezuela (BT-0984); ***2***: Aruba (BT-4964); ***3***: Bahamas (BT-3418); ***4***: Guantanamo, Cuba (BT-2668); ***5***: Lac Bay, Bonaire (BT-3872); ***6***: Guantanamo, Cuba (BT-2669); ***7***: Lac Bay, Bonaire (BT-3874); ***8***: Brevard County, Florida (BT-2764). **9-10**: ***O. fulgurator*** forma ***circinata*** Marrat, 1871. ***9***: Alagoas, Brazil (BT-2114); ***10***: Rio de Janeiro, Brazil (BT-2113). **11-18**: ***O. spicata*** (Röding, 1798).

11: Baja California, Mexico (AB-b207); ***12***: Cebaco I., Panama (BT-3755); ***13***: Baja California, Mexico (BT-4289);

14: Guerrero, Mexico (BT-5335); ***15***: Baja California, Mexico (BT-0346); ***16***: Baja California, Mexico (RF-b06);

17: Baja California, Mexico (BT-4123); ***18***: Baja California, Mexico (AB-b384). **19-20**: ***O.spicata deynzerae*** Petuch & Sargent,1986. ***19***: Cocos Is., Costa Rica (BT-5447): ***20***: Cocos Is., Costa Rica (BT-5446).

21-22: ***O. polpasta*** Duclos, 1840. ***21***: Oaxaca, Mexico (BT-4613, forma *kerstitchi*); ***22***: Cebaco I., Panama (BT-3781). **23-24**: ***O. scripta*** Lamarck, 1811. ***23***: Honduras (BT-2756); ***24***: Haiti (BT-2379).

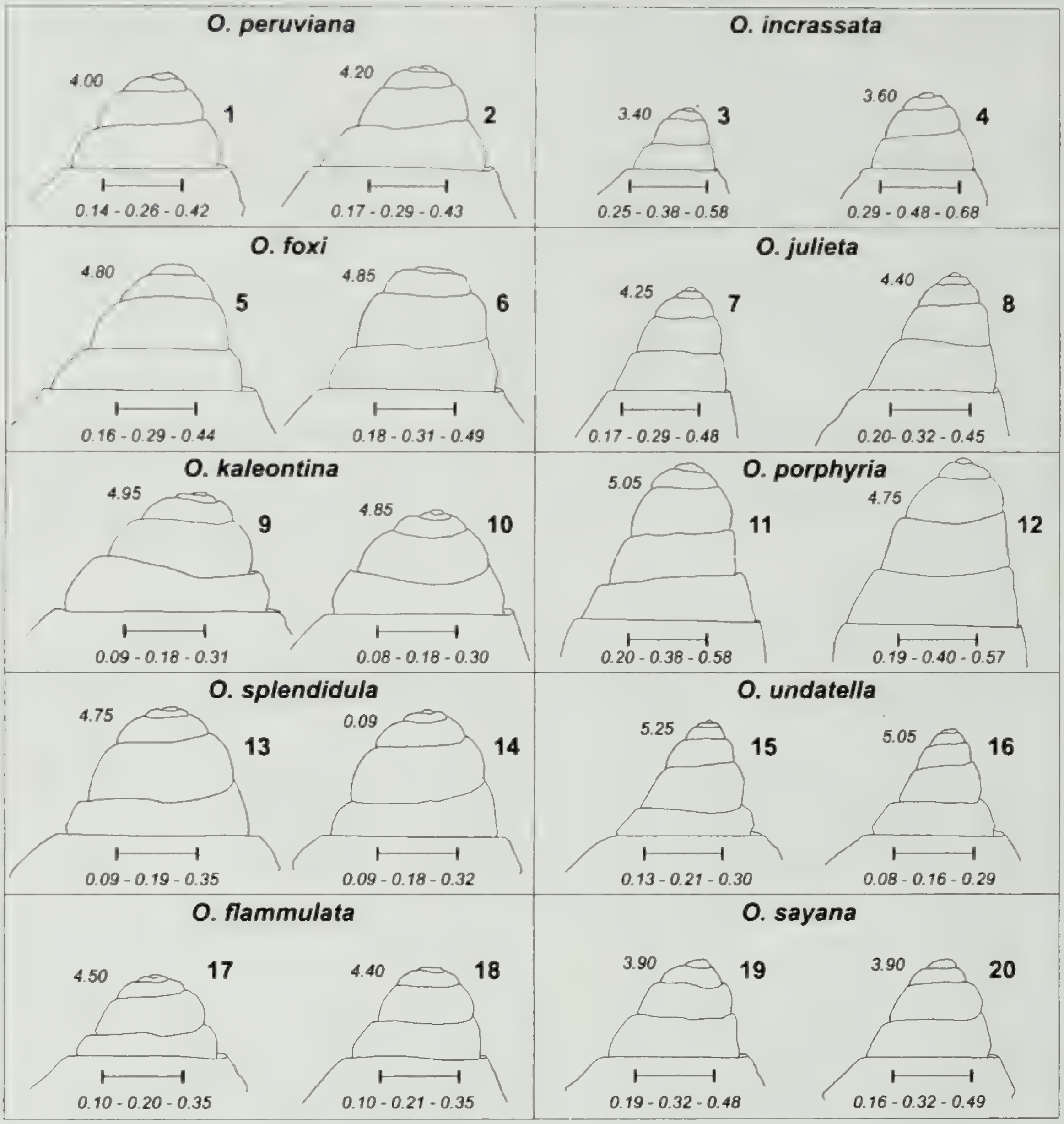

Fig. 9. **Protoconchs (Eastern Pacific)**. Scale bars: 1 mm. Figures to the left of apex: number of nuclear whorls (NW). Figures below scale bar: measurements SPRO, MPRO and LPRO of first protoconch volutions (see Fig. 2). **1-2**: ***O. peruviana*** Lamarck, 1811. ***1***: Iquique, Chile (BT-5785); ***2***: Iquique, Chile (BT-5784). **3-4**: ***O. incrassata*** (Lightfoot in Solander, 1786). ***3***: Puerto Penasco, Mexico (DG-4224/3);***4***: Michoacan, Mexico (DG-4224/2).

5-6: ***O. foxi*** Stingley, 1984. ***5***: Cocos Is., Costa Rica (BT-3326); ***6***: Cocos Is., Costa Rica (BP-b07).

7-8: ***O. julieta*** Duclos, 1840. ***7***: Michoacan, Mexico (DG-4224/3); ***8***: Michoacan, Mexico (DG-4224/3).

9-10: ***O. kaleontina*** Duclos, 1835. ***9***: Cebaco I., Panama (BT-3751); ***10***: St. James I., Galapagos (BT-4275).

11-12: ***O. porphyria*** (Röding, 1798). ***11***: Gubernadora I., Panama (BT-4464); ***12***: Sonora, Mexico (BT-0346).

12-13: ***O. splendidula*** Sowerby, 1825. ***13***: Perlas Is., Panama (BT-3731); ***14***: Manzanillo, Mexico (BT-4023).

15-16: ***O. undatella*** Lamarck, 1811. ***15***: Colima, Mexico (BT-0331); ***16***: Venado I., Panama (BT-1666).

17-18: ***O. flammulata*** Lamarck, 1811. ***17***: Port Gentil, Gabon (BT-2087); ***18***: Gorée, Sénégal (BT-2127).

19-20: ***O. sayana*** Ravenel, 1834. ***19***: Indian River, Florida (BT-4064); ***20***: Marco Beach, Florida (BT-3108).

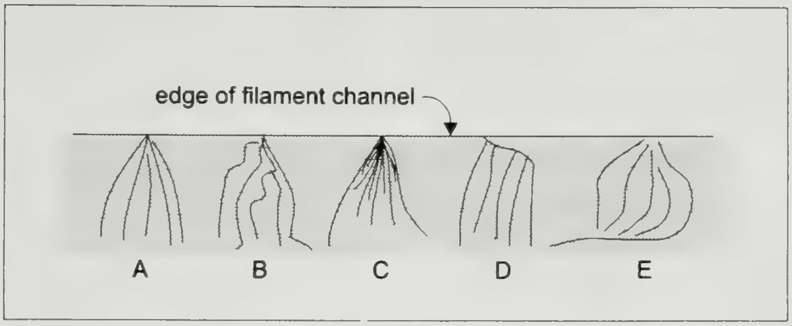

Fig. 10. Some examples of "fasciculated" subchannel colour markings (see § 4.1).

Although some general geographical trends can be noted (see § 4.5), neighbouring populations do not necessarily resemble each other very much. The general distribution of many single characters shows chaotic interdeme variation [like the "*crazy quilt*" distribution observed for *Cerion* by GOULD & WOODRUFF (1978)] and would seem to fairly reflect habitat discontinuities.

4.3. Systematic allotopy.

4.3.1. The "*O. fulgurator-reticularis* complex"

Much time has been spent in interviewing many experienced local collectors (ranging from professional malacologists to fishermen collecting molluscs for the shell trade). All were unanimous in reporting that within the "*fulgurator-reticularis* complex", shells of different forms ('species' ?) are never found living together. This has also been our personal experience during collecting trips in Brazil, Colombia, Mexico, Venezuela and the Virgin Islands. The populations of shells with different forms are invariably *allotopic*.

It is important to stress the restricted meaning of "living together". One could indeed object that some distinct populations can live within short distance (for instance, at least two forms have been reported from Gonave, Haiti, by PETUCH 1986, and at least three different forms live in Aruba. Detailed field studies in the Southern Pacific have demonstrated that completely distinct, conspecific populations of several species have been observed to be separated by only a few hundred meters (VAN OSSELAER *et al.* 1993). The scale of sympatry in the genus *Oliva* is thus much smaller than generally thought (TURSCH 1994) and it should, for safety, be reduced to the scale of *syntopy* (i.e. found living in the same microbiotope, within a distance of meters).

4.3.2. The "*O. spicata* complex"

From all the information we could gather, the same situation is met for the "*O. spicata* complex" in the Eastern Pacific. The only exception known to us is the report by BURCH & BURCH (1962) on the coexistence of the "species" *O. rejecta* Burch & Burch, 1962 (see Section 7, Systematics, under *O. spicata*) with *O. venulata* Lamarck, 1811. The authors wrote: "*Both forms are found on the same tide flats at La Paz, Baja California, Mexico, with no intergrades in many hundreds of specimens*". One will notice the use of the word "*forms*" to designate what the authors consider distinct species. Nevertheless, this had to be taken seriously because, if this coexistence were factual, it could falsify the very premises upon which the conclusions of the present work do rest.

One of us (BT) recently went to La Paz for an *in situ* check of the situation. Large numbers of live specimens were observed at eleven tide flats in Bahia La Paz (see map, Pl. 2) (*e.g.* 78 specimens at Punta de Leon, 129 at Herendira, 318 at Balandra). The previous observations made in the Caribbean and in the South Pacific were fully verified: all the *Oliva spicata* populations that were seen were local morphs, with cryptic colouration (matching that of the substrate), and quite homogeneous in characters. No form absolutely identical to the "real" *O. rejecta* was not found (although the Herendira population is quite similar, see Pl. 2). It might live in another of the very numerous isolated bays of the region (their systematical study would take very considerable time). Or its habitat may have been destroyed (the original beaches of La Paz City are said to have been washed away after the construction of the Malecón, many years ago; the sand of the present beaches is imported).

Around La Paz, *Oliva spicata* is collected (overcollected?) in large quantities for the tourist trade. So the conclusions from our field observations were fully confirmed by the examination of well over 100 kilos of specimens in the possession of local fishermen (one single person had a lot of 60 kilos -estimated at over 8000 specimens). None of the local collectors (some gathering *O. spicata* for over 25 years) could remember a single case of co-occurrence of different forms.

It would thus seem that BURCH & BURCH were simply given incorrect locality data (as it only too often happens for commercial specimens) and that the case of *O. rejecta* cannot be construed as a counter-example.

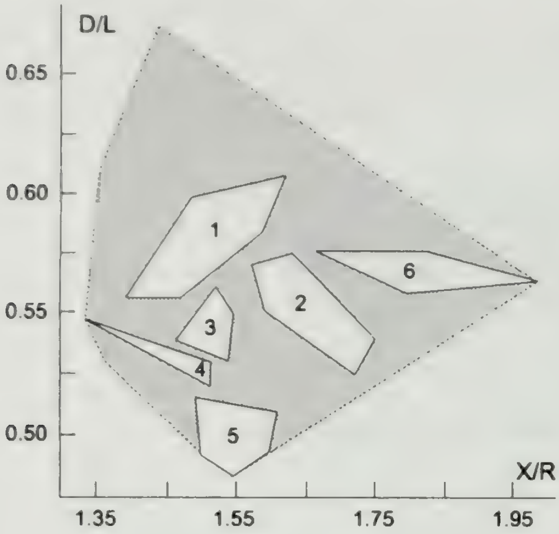

Fig. 11. Example of total separation of selected local samples within the "*O. fulgurator-reticularis* complex" (gray zone). Scatter diagram: X/R vs. D/L . Minimum convex polygons. **1.** CURAÇAO, (*O.* cfr. *nivosa* Marrat); **2.** PUERTO RICO (*O. reticularis* Lamarck); **3.** BARBADOS, deep water (*O. barbadensis* Petuch & Sargent); **4.** BERMUDA (*O. bifasciata jenseni* Petuch & Sargent); **5.** BRAZIL, Bahia (*O. circinata* Marrat); **6.** VENEZUELA, Margarita I. [*O. fulgurator* (Röding)].

4.4. Morphological continuum.

Much effort (research on this project started in 1987) has been invested in trying to break the "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" into objective subgroups, mainly by using the methods already applied to the Indo-Pacific "*O. miniacea* complex" based upon *O. miniacea* (Röding, 1798) (TURSCH & GREIFENEDER 1996). All these attempts (many combinations of variables were tested) failed consistently.

In the Western Atlantic, all the local populations of the "*O. fulgurator-reticularis* complex" can be objectively separated from some (or even many) others, as illustrated by the scatter diagrams of Figs. 11 and 12. The same situation is met in the Eastern Pacific for the members of the "*O. spicata* complex", as illustrated in the scatter diagrams of Fig. 13.

These separations are invariably obliterated by the inclusion of some additional population(s). As one example amongst many, Fig. 14 groups the populations previously separated in Figs. 11 and 12, with the addition of only four other local samples. Every one of these distinct populations is now linked to every other by an unbroken chain of intermediates, forming a continuum.

Even without any measurement, the existence of a continuum can be sensed just by glancing at Plates 6, 7, 8 and 9, in which the type material of the various taxa constituting the "*O. fulgurator-reticularis* complex" has been arranged by grouping specimens according to resemblance. These plates, however, give only a limited view of the total variation range because many local forms have not been described.

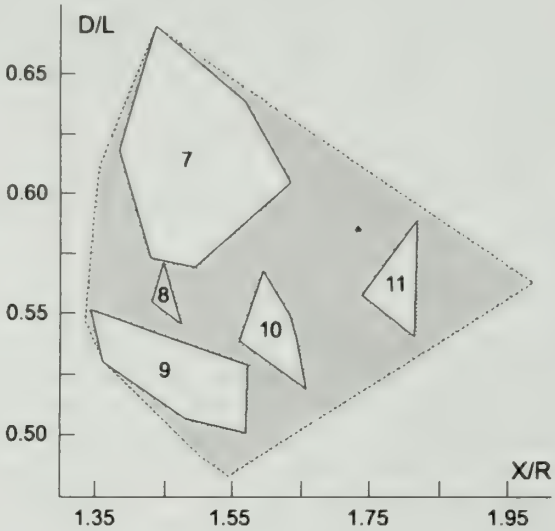

Fig. 12. Example of total separation of selected local samples within the "*O. fulgurator-reticularis* complex" (gray zone). Scatter diagram: X/R vs. D/L (same variables as in Fig. 11). Minimum convex polygons. **7**. CUBA, Guantanamo (unnamed form); **8**. ST. MARTIN (*O. nivosa* Marrat); **9**. FLORIDA, off Punta Vadra, deep water (*O. bollingi* Clench); **10**. COLOMBIA, Santa Marta (*O. goajira* Petuch & Sargent): **11**. VENEZUELA, Paranaguá Peninsula [*O.* cfr. *fulgurator* (Röding)].

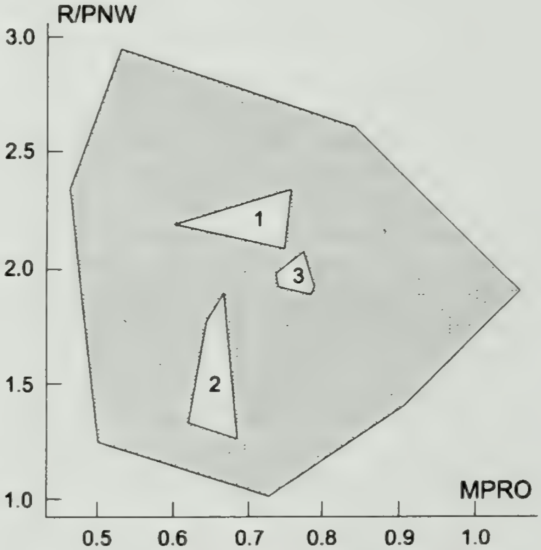

Fig. 13. Example of total separation of selected local samples within the "*O. spicata* complex" (gray zone). Scatter diagram: MPRO vs. R/Pnw. Minimum convex polygons. **1.** PANAMA, Bayarena, 20-30 m. **2.** MEXICO, Baja California, La Paz, shallow water; **3.** COCOS Is., 12-20 m (*O. spicata deynzerae* Petuch & Sargent).

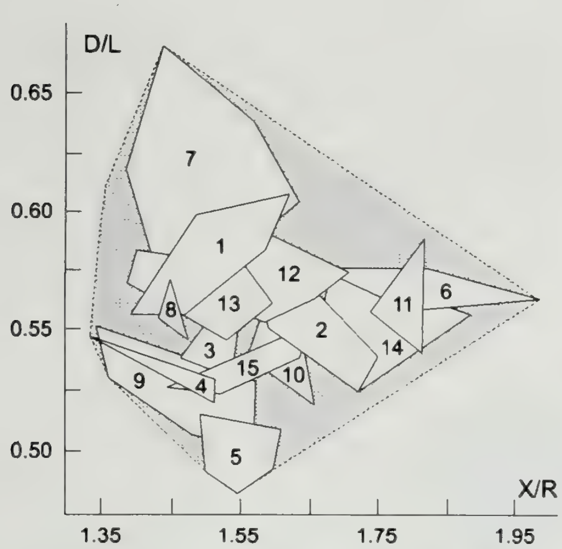

Fig. 14. Local populations within the "*fulgurator-reticularis* complex" (gray zone) form a morphological continuum: an example. Same variables and populations as in Figs. 11 and 12, 4 populations added: 12 to 15. Scatter diagram: X/R vs. D/L). Minimum convex polygons. **1.** CURAÇAO, (*O.* cfr. *nivosa* Marrat); **2.** PUERTO RICO (*O. reticularis* Lamarck); **3.** BARBADOS, deep water (*O. barbadensis* Petuch & Sargent); **4.** BERMUDA (*O. bifasciata jenseni* Petuch & Sargent); **5.** BRAZIL, Bahia (*O. circinata* Marrat); **6.** VENEZUELA, Margarita I. [*O. fulgurator* (Röding)]; **7.** CUBA, Guantanamo (unnamed form); **8.** ST. MARTIN (*O. nivosa* Marrat); **9.** FLORIDA, off Punta Vadra, deep water (*O. bollingi* Clench); **10.** COLOMBIA, Santa Marta (*O. goajira* Petuch & Sargent): **11.** VENEZUELA, Paranaguá Peninsula [*O. fulgurator* (Röding) variant]; **12.** DOMINICAN REPUBLIC (*O. jamaicensis zombia* Petuch & Sargent); **13.** HONDURAS (*O.* aff. *ernesti* Petuch); **14.** ARUBA (*O.* cfr. *sargenti* Petuch); **15.** ST. VINCENT (unamed, dark form).

Petuch & Sargent (1986: 119-122) claimed that, "based on shell morphology", the taxa we here place in the "*O. fulgurator-reticularis* complex" break up into groups: the *reticularis* group ("characterized as being ovate shells with rounded outlines and by having variable amounts of triangle net color patterns"), the *bifasciata* group ("slender, cylindrical, elongated shells with fairly straight sides"), the *nivosa* group ("elongated shells with straight or slightly rounded sides ... flattened spires and intricate, fine-netted color patterns") and the *tisiphona* group (said to " ... resemble the Panamic *O. spicata* and *O. incrassata* groups"). We could find no basis whatsoever on which to segregate the above groups.

Exactly the same situation was observed for the "*O. spicata* complex". As one example amongst many, Fig. 15 adds just two other local samples to the populations previously separated in Fig. 13. Here again, one sees the formation of a continuum.

In conclusion: we have found no way of separating any of the populations (or group of populations) from <u>all</u> the others. The "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" each consist of a *morphological continuum* of local forms (see § 3.3).

4.5. Clinal variation.

Although neighbouring populations do not necessarily resemble each other (see § 4.2), the populations of the "*O. fulgurator-reticularis* complex" display a quasi-clinal variation of *some* characters, such as the protoconch size. This can be seen, for instance, in Fig. 16, showing the distribution of the largest local measurements of PAT18 (the diameter of the penultimate nuclear volution, see Fig. 2).

This quasi-clinal variation, from Northern South America outwards, is not restricted to protoconch characters but is also reflected in the general shape of shells. Globose shells (*O. fulgurator s.s.*) are found only around Venezuela and Aruba, whereas more cylindrical, elongated shells are found at both ends of the distribution range, in Brazil (the form *circinata*) and in Florida. Here again, the variation is roughly clinal, as shown in Fig. 17, the distribution of the largest local measurements of D/L (breadth of the body whorl relative to the length of the lip). A quite similar clinal distribution (not illustrated here) is observed for the mean values of D/H.

No such clines have yet been observed for the forms of the "*O. spicata* complex", in the Eastern Pacific.

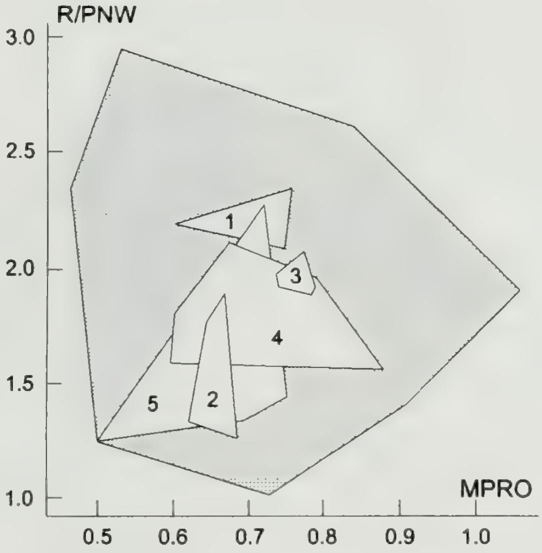

Fig. 15. Local variants within the "*O.spicata* complex" (gray zone) form a morphological continuum: an example. Same variables and populations as in Fig. 13, 2 populations added: 4 and 5. Scatter diagram: X/R vs. D/L). Minimum convex polygons. **1.** PANAMA, Bayarena, 20-30 m. **2.** MEXICO, Baja California, La Paz, shallow water; **3.** COCOS IS., 12-20 m (*O. spicata deynzerae* Petuch & Sargent). **4.** MEXICO, Baja California, Santa Rosalia, shallow water; **5.** PANAMA, Cebaco I., 35-40 m.

Fig. 16. "*O. fulgurator-reticularis* complex". Clinal variation of the protoconch measurement PAT18. Distribution of maximal observed values (see text § 4.5). Only a few values are given, for clarity. The values for isophene lines are arbitrary.

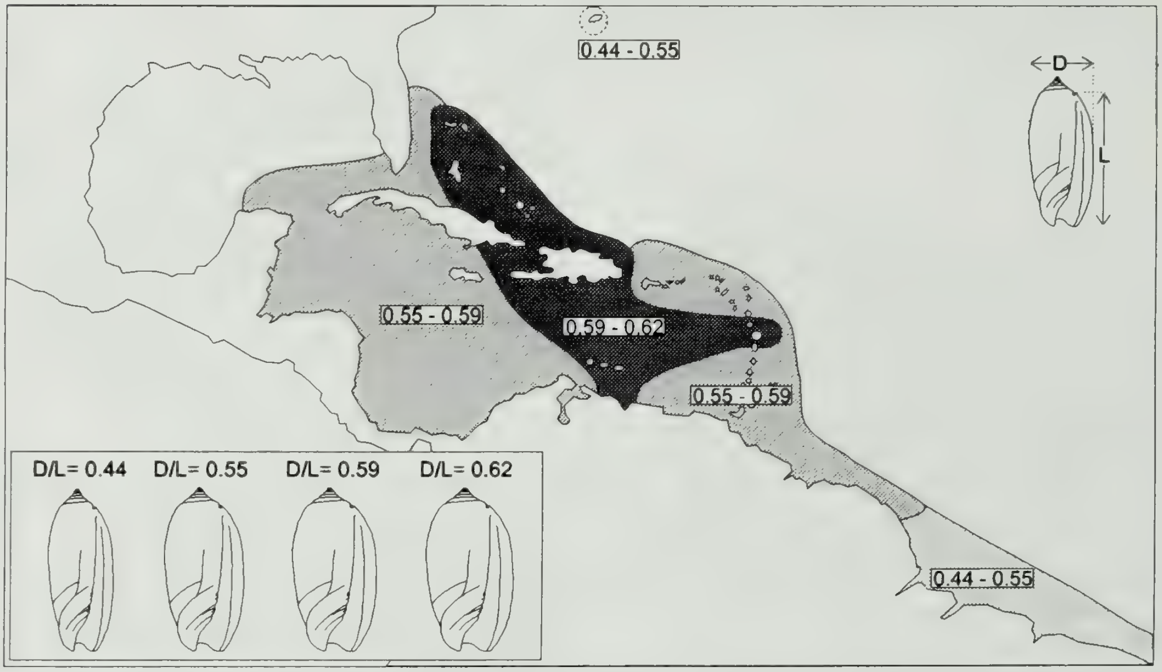

Fig. 17. "*O. fulgurator-reticularis* complex". Clinal variation of the teleoconch character D/L. Distribution of maximal observed values (see text § 4.5). Only a few values are given, for clarity. The values for isophene lines are arbitrary.

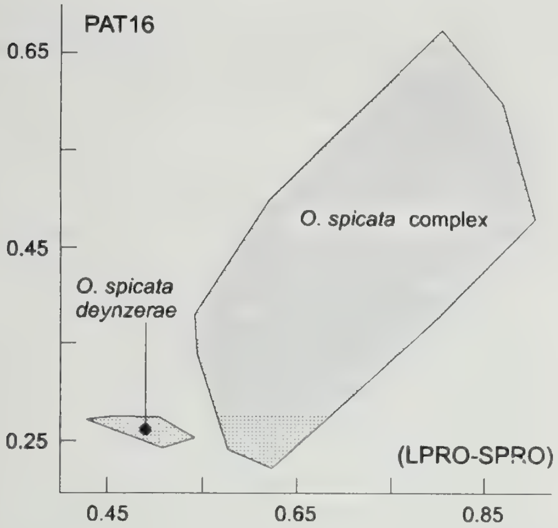

Fig. 18. "*O. spicata* complex". Separation of *O. spicata deynzerae*. Scatter diagram: PAT16 vs. (LPRO-SPRO). Minimum convex polygons. See text § 5.3.

5. INTERPRETATION

5.1. *Oliva fulgurator* (Röding, 1798).

Three independent arguments indicate that all the cognate taxa forming the "*O. fulgurator-reticularis* complex" constitute one single, highly variable species. We are certainly not the first to reach this conclusion:

> "*Ol. fusiformis*, Lam. [the former name for *O. fulgurator* (Röding)], is a shell that appears characteristical when one has only *types*, but one finds all possible intermediates and we do not understand why Mr. Reeve did not propose its reunion with *reticularis*, as he has done for others."
>
> DUCROS DE SAINT GERMAIN (1857: 54)
> (*translation ours*)

The first argument is purely phenetic. In spite of much effort to that end, none of the taxa constituting the "*O. fulgurator-reticularis* complex" (cited in the synonymy of *O. fulgurator*) could be separated from *all* the others on the basis of shell measurements. The range of variation of both the teleoconchs and the protoconchs is quite extraordinary for the genus *Oliva*, but all intermediate forms are present. The various populations form a morphological continuum (see § 4.4). Analysis of the colour patterns of the shells fully confirms this view.

The second argument is based on distribution data. All the taxa constituting the "*O. fulgurator-reticularis* complex" are systematically allotopic (see § 4.3). This mutual exclusion of so many *Oliva* 'species' is highly unusual. It is well known to anyone who has collected in the Indo-Pacific that most (if not all) species of *Oliva* are found together with other, congeneric species. Up to 12 species of *Oliva* have been observed to live together in the same microhabitat in Hansa Bay, Papua New Guinea (VAN OSSELAER *et al.* 1993). PETUCH & SARGENT (1986) report that "over twenty" *Oliva* species can be found living together in some Indo-Pacific localities. So, one must now ask the question: "How can we explain that the many Caribbean 'species' of the '*O. fulgurator-reticularis* complex' do **never** occur together?" The simplest (and most likely) answer is that they are not different species but only local populations of the same species.

A third, independent argument for the conspecificity of all the populations forming the "*O. fulgurator-reticularis* complex" stems from the quasi-clinal variation of some shell characters over the distribution area (see § 4.5). It is most improbable that the observed pattern of variation reflects an environmental cline. The 1.20-1.39 mm isophene zone in Fig. 16, for instance, stretches over very varied types of sediment, in very diverse physical conditions. An interpretation in terms of clinal gene variation within a same species is much more likely. Note: the observed pattern (of central populations being distinct from Northern and Southern populations which resemble each other) appears to be rather common in other zoological groups. It is familiar to ornithologists under the name of "leapfrog" pattern of geographic variation (see REMSEN 1984).

The differences in protoconch size observed between extreme forms of the "complex" are much greater than in any other *Oliva* species we know of. This does not indicate separate specific status, the range of variation being continuous.

Many of the populations forming the species are today commonly referred to as *O. reticularis* Lamarck, 1811, although the original concept of the species was propably quite different (see the section Systematics). We are nevertheless compelled to use the name *O. fulgurator* (Röding, 1798), which has priority, notwithstanding that it originally designated and is still commonly used for a form which has a restricted distribution and is less common in collections.

5.2. *Oliva spicata* (Röding, 1798).

As in the case of *O. fulgurator* (Röding, 1798), all the examined populations of the "*O. spicata* complex" (save one, see § 5.3) form one single, compact morphological continuum (see § 4.4). We have therefore to consider these populations as members of one same species: *Oliva spicata* (Röding, 1798). Here also, the range of variation of both the shells and the protoconchs is quite extraordinary for the genus *Oliva*, but all forms are linked by intermediates. Analysis of the colour patterns of the shells does again fully confirms this view.

5.3. *Oliva spicata deynzerae* Petuch and Sargent, 1986.

This taxon (see PL. 4, FIG. 5) is restricted to the Cocos Islands and appears to be very closely related to *Oliva spicata* (Röding, 1798). It is nevertheless objectively separated from *all* other forms of the "*O. spicata* complex" in a scatter diagram of LPRO-SPRO *vs.* PAT16 (see Fig. 18). Very similar results are obtained with scatter diagrams of SUT/L *vs.* PAT16 and of NW *vs.* PAT16 (not illustrated), the major discriminant being PAT16.

The separation gap is narrow and rests upon a rather small sample (7 only specimens of the Cocos Is. taxon), so it is not impossible that the observed gap could be filled by additional specimens. We shall follow the advise of MAYR & ASQUITH (1991: 37) on such cases (allospecies) and attach the Cocos Is. population as a subspecies (*deynzerae* Petuch and Sargent, 1986) to its closest relative, *O. spicata* (Röding, 1798).

5.4. *O. spicata* and *O. fulgurator*: separate species?

It has been seen (§ 4.1, fig. 7) that the Eastern Pacific "*O. spicata* complex", as a whole, could not be objectively separated on morphometrical grounds from the Western Atlantic "*O. fulgurator-reticularis* complex". Were it not for the existence of the Panama land bridge, one would have little choice but to combine the two complexes into one single morphospecies. This logical step was indeed taken long ago by DUCROS DE SAINT GERMAIN (1857: 52-56), at a time when the locality data of most shells were unreliable. His *O. reticularis* Lamarck, 1811 –which he considered to have a nearly world-wide distribution– included a long list of taxa, known today to be restricted either to the Eastern Pacific or the Western Atlantic faunas.

Within the biological species concept, we cannot anymore take such a simple stand (and we find ourselves in the general problem of species with a discontinuous distribution). The two "complexes" cannot anymore meet to possibly interbreed, and have now been separated by the Panama land barrier for an estimated 1.6 million years (see PETUCH & SARGENT 1986: 119). Therefore, as a working hypothesis until tested by genetic studies, the "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" will be here considered as distinct species.

The two complexes certainly share a common ancestry and constitute one more example of the many pairs of 'geminate species', sister taxa of which one element is present in the Panamic region, the other in the Caribbean. In nearly all cases, these 'sister taxa' are considered to now form distinct species. Final closure of the waterway linking the Pacific to the Atlantic occured about 1.6 Ma (millions years ago) according to PETUCH & SARGENT (1986: 119), 3.1-2.8 Ma according to COATES & OBANDO (1996: 21), in any case an acceptable "divergence time " for species separation (see COLLINS 1996). Today, the Caribbean and the Panamic regions are not only geographically separated; they constitute two strikingly different realms. Southern Caribbean waters are in average 2° C warmer and 1.5 ‰ more saline than those of the eastern equatorial Pacific. The latter, in addition, have strong seasonal upwellings causing large increases in primary productivity (see TERANES, GEARY & BEMIS 1996). The eastern equatorial Pacific also has much stronger tides, is subject to El Niño southern oscillation climate anomalies, more intense predation and a much poorer coral reef development (see JACKSON, JUNG & FORTUNATO 1996).

Populations of the "*O. fulgurator-reticularis* complex" (Western Atlantic) often differ amongst themselves as much as they differ from populations of the "*O. spicata* complex" (Eastern Pacific). But the two "complexes", although not objectively separable by shell measurements, do nevertheless have different trends. In general, Panamic specimens have a more puncticulated colour pattern on the body whorl (the starting point of the chevrons is marked by a dark spot). In addition, the body whorl is often more angular at the lip (this is not detectable by our measurements), the "*bifasciata* colour pattern" with two sharply contrasting dark, spiral bands (see Pl. 99, Fig. 99) is absent (or at least very rare), while all dark (melanistic?) specimens are much more frequent.

So, albeit a few cases could lead to confusion, the experienced *Oliva* student does today rarely err in separating Atlantic from Panamic specimens. In most instances, it is quite possible that we just recognise well-known localities, characterized by familiar forms, instead of using reliable, objective discriminants at the species level. Errors in separation were much more common one century ago. Many kinds of shells were then available (possibly more than today, due to the variety of ports of call of the sailing ships) but their origin was uncertain (see § 1.1.2) and no reliable conclusions could be drawn.

Taxonomic distinction of non objectively separable taxa of on the basis of evident geographic isolation is not restricted to taxa separated by the Central American land barrier and is now widely admitted. For instance, the Panamic *Conus dalli* Stearns, 1873 and the Indo-Pacific *C. textile* L., 1758 are not separable (according to A. KOHN, private communication 1997).

6. DISCUSSION

6.1. Partial isolation of populations.

The most striking characteristic of the "*O. fulgurator-reticularis* complex" and the "*O. spicata* complex" is the high endemism of mutually exclusive local forms (many of these forms have been named). This has also been recognized by others. For instance, Petuch & Sargent (1986: 120), refering to their "*bifasciata* group" (see $ 4. 4) say that "Many of these species are endemic to isolated seamounts and deep water pockets".

The situation is far from being unique in the genus *Oliva*. Within the distribution limits of the species, and provided the species is present, every isolated little beach of the Indo-Pacific that we have examined appears to have one (and only one) local form of *O. oliva* (L., 1758). Many of these local forms are quite recognisable. Of course, intrapopulation variants are common, but these are linked by sympatric (syntopic) intergrades. This is the best argument for saying that *O. oliva* is only one species (all populations forming one single morphological continuum). Very similar cases are provided by *O. miniacea* (Röding, 1798), *O. amethystina* (Röding, 1798) and many other *Oliva* species. We are just lucky that many of these local Indo-Pacific forms have not yet been named as species or subspecies.

One possible explanation is genetic. Such a situation can occur if successful, long-distance transport and settlement of the larvae is frequent enough to allow occasional gene flow between conspecific populations but rare enough to allow some genetic drift of the local isolates. The efficiency of larval transport and settlement will of course vary from species to species; if it is highly efficient there will be little local variation. Many *Oliva* species [for instance *O. splendidula*, *O. porphyria*, *O. caerulea* (Röding, 1798)] are indeed very constant over all their distribution range.

Another explanation would be to consider that the different local populations are only ecotypes, arising from the expression of a same genotype in different local environments. In this hypothesis, larval transport should play a secondary role, if any. The great number of local forms within many *Oliva* species would also imply an extraordinary sensitivity to minute environmental changes.

Distribution data support the first, genetic hypothesis. No *Oliva* species has been reported from Clipperton Island (EMERSON, 1994), or from the Revillagigedo Islands (EMERSON, 1995), distant of about 600 and 375 miles from Mexican mainland, respectively. The much larger Galapagos (see FINET 1991) –about 600 miles from the mainland– have two species [*O. porphyria* (Linnaeus, 1758) and *O. kaleontina* Duclos, none belonging to the "*O. spicata* complex"]. The somewhat less isolated Cocos islands (about 300 miles from the mainland) have one endemic species (*O. foxi* Stingley, 1984) and one endemic subspecies (*O. spicata deynzerae* Petuch & Sargent, 1986). This indicates a weak efficiency of successful, long-distance transport and settlement of larvae in the "*O. spicata* complex". Established populations generally contain large numbers of individuals, so the effect of ocasional larvae immigration can be expected to be rapidly diluted in a large gene pool.

Dr. P. E. PENCHASZADEH (private communication) together with Dr. Juan DIAZ, observed and collected in small islands off Venezuela several specimens of a form of "*Oliva circinata*" laying long ribbons of eggs, anchored in the substrate. This phenomenon (not reported yet for other *Oliva* species) could explain the great endemism of local forms, larval development of *Oliva* being known to occur within the egg capsule (OLSSON & CROVO 1968).

The "crazy-quilt" distribution pattern of local populations is not unique to *Oliva* species. A similar pattern is observed for many taxa of *Conus* in the Cabo Verde region and for many forms of *Cymbiola (Cymbiolacca) pulchra* in Queensland, Australia (POPPE & GOTO, 1992). Stable differences between allopatric populations were reported by PARTH (1995) for taxa of the muricid genus *Haustellum* .

6.2. Dynamic environment.

One can quite safely assume that speciation in the genus *Oliva* follows the normal, allopatric (or vicariant) process (see Fig. 19, a, b). This starts by the advent of a geographical barrier restricting the gene flow between populations of a same species. These populations (now partially or totally isolated) will then undergo divergent evolution, possibly to the point where they cannot interbreed any more when brought back into contact. Once started, the speciation process is not irreversible. It might abort for a variety of causes (see Fig. 19, c), for instance if the geographical barrier does not persist long enough (which is precisely the case advocated here above). In any case, speciation is not a sudden event. The process takes place over a large number of generations and there is necessarily a period in time during which the speciation issue is undecided.

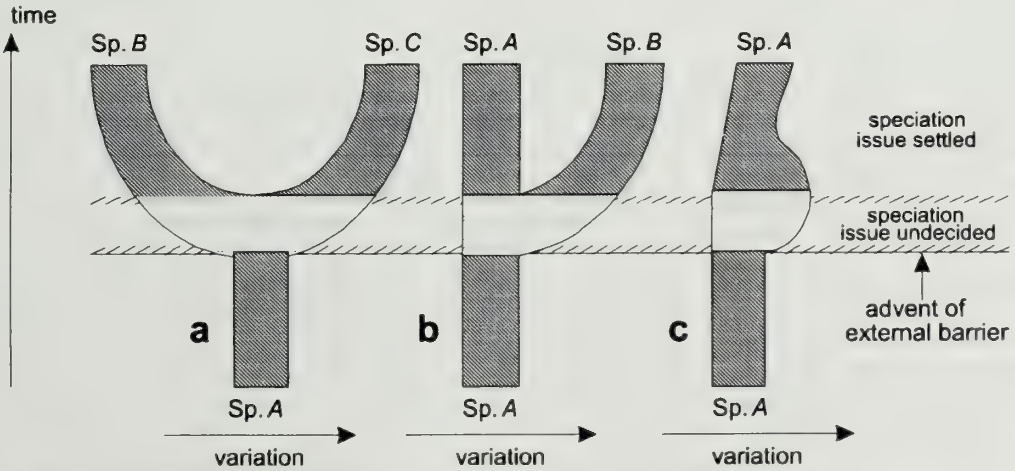

Fig. 19. The problem of incipient species. **a**: speciation by splitting (allopatric speciation by vicariance). **b**: speciation by budding (peripatric speciation). **c**: aborted speciation. See text § 6.2.

The recent geological history of the Caribbean region is one of many important variations of the sea-level, resulting in huge modifications of the coastlines. The Western Atlantic and the Eastern Pacific regions were repeatedly linked by seaways, then isolated again by emergences of the Panama Isthmus. Many Caribbean islands were also repeatedly separated, then reunited, sometimes into new combinations [see maps figs. 3 (p. 61), fig. 5 (p. 65), fig. 11 (p. 109), fig. 12 (p. 111), fig. 13 (p. 113), fig. 14 (p. 125) in PETUCH 1988; also maps 2.9 and 2.10 in COATES & OBANDO, 1996)].

These geological circumstances provided an ideal stage for a scenario of repeated isolations of populations, reflected in morphological changes (due to genetic drift or/and ecological factors). These episodes of isolation were followed by reunions (and aborted speciations and introgressions). This history also allowed geographical heterochrony –the persistence of Neogene faunas in "relict pockets" into the Recent fauna, [PETUCH 1982, PETUCH 1988: 149-200, map fig. 19 (p. 168)]. In response to such a dynamic geography, *Oliva* species in which succesful, long-distance larval transport and settlement of larva is of weak efficiency (see above, § 6.1), can become highly dynamic in their morphological evolution. It is known that changes can be rapid: one example has been reported of a small isolate of an *Oliva* species [*O. amethystina* (Röding, 1798)] undergoing detectable morphological modifications within the time span of a few decades (TURSCH 1994).

6.3. Nomenclature: fixed names for dynamic species.

It could be argued that populations between which the gene flow is restricted are *incipient species* and should therefore be named. It is of course conceivable that some pairs of such populations, if brought into contact, could not interbreed anymore but we have yet no factual evidence to that point.

An apparent paradox is that, when the speciation issue is undecided, the nomenclatural situation is not. As said by DAWKINS (1996: 96): "*In a way, our naming procedures are set up for a pre-evolutionary age when divides were everything and we did not expect to find intermediates"*. In any case, the Code of Nomenclature simply has no provision for *hypothetical*, future species. If one wishes to draw attention to such cases, the best one can do is using infrasubspecific (form) names, which have no nomenclatural standing.

7. SYSTEMATICS

In this section, the names of very frequently cited authors will be abbreviated, to save on space. So, B. & B. stands for BURCH & BURCH, P. & S. for PETUCH & SARGENT, W. & A. for WAGNER & ABBOTT, Z. & P. for ZEIGLER & PORRECA. To avoid confusion, "Pl." and "fig(s)." refer to plates and figures in cited works, while "PL." and "FIG(S)." refer to illustrations in the present paper. The abbreviation "*q.v.*" (*quod vide*) means "*see under that name*".

Throughout this text, the convenient device of a semicolon inserted between the specific name and the author [*X-us albus* ; Smith (not Brown)] is used to distinguish between a misidentification, which has no nomenclatural status, and a homonym [*X-us albus* Smith (not Brown)], which has (see MAYR & ASHLOCK 1991: 362).

The taxonomical status of every name has been discussed separately. This entails much repetition but allows the reader to inquire about a particular taxon without having to read all the text.

In deference to conchological tradition, the following "Description" paragraphs are largely based upon shell ornamentation, which is notoriously variable in the genus *Oliva*. So, these sections can serve *only* for quick identification. The species have ***not*** been delimited on these characters but on morphometrics (see § 4 and 5). This exploratory task being accomplished, detailed measurements are generally not indispensable any more for identification of individual specimens. All characters common to the genus (shell smooth, shiny, etc.) have been omitted and only features with some discrimination power are reported. Preference has been given to details possessing probably very little or no adaptative value. As just stated here above, very few (if any) of these traits, taken one by one, will allow secure identification of an individual specimen. The probability for achieving this will be much increased by observing the simultaneous presence of such features. *Oliva* species, although highly variable, have nevertheless limited "*répertoires*". Familiarity with the limits of intraspecific variation should allow rapid identification of most (but not all) specimens.

Family **OLIVIDAE** Latreille, 1825

Subfamily OLIVINAE Latreille, 1825

Genus *Oliva* Bruguière, 1789

Oliva foxi **Stingley, 1984.**

Oliva foxi Stingley, 1984: 28.

Description.

SIZE: up to about 40 mm.

SHAPE: fusiform-elongated.

SPIRE: conical, elevated, with large spire callus, uniformly purple-gray to beige, covering ½ to 4/5 of the whorl.

CHANNEL: rather narrow.

SUBCHANNEL PATTERN: fasciculated, of short brown stokes.

SHELL BACKGROUND: pale cream to whitish.

COLOUR PATTERN: Faint pink tent pattern overlaid with distinct dark brown triangular areas, speckled with white tents, and heavy brown lines, formed of rows of small isoscele triangles.

COLUMELLA: white, with faint purple base.

SUPRAFASCIOLAR BAND: lower half with chevron-like brown marks.

APERTURE: suffused with orange-saffron. Inner margin of lip milky white.

PROTOCONCH: pink to bright purple-pink.

Diagnosis. Distinguished from all other American *Oliva* by its unmistakable, outstanding colour pattern, saffron aperture and small size.

Distribution. Known only from 18 m, white sand, Cocos Islands, Costa Rica.

Oliva foxi Stingley, 1984. This taxon, broadly sympatric with *O. spicata deynzerae* is easily separated from all members of the "*O. spicata* complex" (see fig. 3) and is an **objective species** (see § 4.1), in agreement with the conclusions of P. & S. (1986). No synonyms. The holotype (see PL. 4, FIG. 1) has been previously illustrated by KAICHER 1988 (Part III, card no. 5249). Three paratypes are illustrated (see PL. 4, FIGS. 2-4). This species has been placed by PETUCH & SARGENT (1986: 123) in their "*splendidula* group", the argument being: "Both shells exhibit a very hig gloss and colour patterns that include bright pinks and purples and wide bands of dark brown. Both species also have yellow or orange apertures".

Oliva fulgurator (Röding, 1798).

Porphyria fulgurator Röding, 1798: 36, sp. no. 453.

Oliva ispida (Link) (not Röding, 1798), 1807: 96:
Oliva fusiformis Lamarck, 1811: 318, sp. no. 30; *Encycl.* Pl. 367, figs. 1a, 1b.
Oliva reticularis Lamarck, 1811: 314, sp. no. 16. *Encycl.* Pl. 361, figs. 1a,b.
Oliva olorinella Duclos, 1835: Pl. 6, figs. 15-16; text in *Illustr. Conch.*: 14 (*pars*).
Oliva obesina Duclos, 1840: Pl. 16, figs. 9-11, text in *Illustr. Conch.*: 26.
Oliva timoria Duclos, 1840: Pl. 17, figs. 11-13; *Illustr. Conch.*: 19 (*pars*).
Oliva aldinia Duclos, 1845: 25, Pl .26, figs. 6-7.
Oliva broderipi Ducros de St.Germain, 1857: 62, sp. no. 39, Pl. 2, 39,a,b.
Oliva jamaicensis Marrat, 1867: 213-15.
Oliva oblonga Marrat, 1867: 215.
Oliva pallida Marrat, 1867: 215.
Oliva bewleyi Marrat, 1870: 7, sp. no. 25, fig. 44.
Oliva figura Marrat, 1870: sp. no. 26, fig. 45.
Oliva formosa Marrat, 1870: sp. no. 16, figs. 29, 30.
Oliva graphica Marrat, 1870: sp. no. 18, Pl. 3, fig. 36.
"*Oliva oblongata* Marrat, 1870" (auct).
Oliva porcea Marrat, 1870: 6, sp. no. 19, Pl. 3, fig. 35.
Oliva olivacea Marrat, 1870: 7, sp. no. 28, Pl. 4, figs. 46-47, 51-53.
Oliva hepatica ; Marrat (not Lamarck, 1811), 1871: sp. no. 14, Pl. 3, figs. 27-28.
Oliva bullata Marrat, 1871: 40, sp. no..215, Pl. 24, fig. 448.
Oliva circinata Marrat, 1871: sp. no. 109, Pl. 17, fig. 277.
Oliva mercatoria Marrat, 1871: sp. no. 111, Pl. 17, figs. 268-269.
Oliva nivosa Marrat, 1871: sp. no. 112, Pl.17, fig. 276; Pl. 25, fig. 472.
Oliva reclusa Marrat, 1871: sp. no. 27, Pl. 17, fig. 264.
Oliva bifasciata Küster in Weinkauff, 1878: 38, sp. no. 35, Pl. 5, fig. 11; Pl. 10, figs. 10, 11.
Oliva cribraria Marrat, 1883?. Published in ... ?
Oliva reticularis bollingi Clench, 1934: 142, Pl. 7, figs. 3, 4.
Oliva reticularis greenwayae Clench, 1937: 17-26.
Oliva pattersoni, Clench, 1945 4: 49.
Oliva drangai Schwengel, 1951: 117, Pl. 8, figs. 2-3.
Oliva antillensis Petuch & Sargent, 1986: 124, Pl. 20, figs. 11, 12.
Oliva bahamasensis Petuch & Sargent, 1986: 125, pl. 20, figs. 15-18.
Oliva barbadensis Petuch & Sargent, 1986: 126, pl. 20, figs. 19-22.
Oliva bifasciata jenseni Petuch & Sargent, 1986: 128, Pl. 21, figs. 16, 17.
Oliva finlayi Petuch & Sargent, 1986: 129, Pl. 22, figs. 5-7.
Oliva goajira Petuch & Sargent, 1986: 133, Pl. 23, figs. 1 2, 13.
Oliva jamaicensis zombia Petuch & Sargent, 1986: 136, Pl. 24, figs. 17, 18.
Oliva magdae Petuch & Sargent, 1986: 138, Pl. 25, figs. 1-3.
Oliva bifasciata sunderlandi Petuch, 1987: 28, Pl. 3, figs. 13, 14.
Oliva circinata tostesi Petuch, 1987: 141.
Oliva sargenti Petuch, 1987: 105, Pl. 17, figs. 2, 3.
Oliva maya Petuch & Sargent, 1986: 139, Pl. 25, figs. 4, 5, 8, 9.
Oliva contoyensis Petuch, 1988: 54, Pl. 32, figs. 12, 13.
Oliva ernesti Petuch 1990: 63, figs. 19, 20.

Description. Within local populations the shells are quite homogeneous. The ranges of variations here under refer to differences *between* populations.

SIZE: from about 25 mm to over 70 mm.

SHAPE: very variable, from elongated-fusiform to nearly cylindrical, to globose.

SPIRE: conical to telescopic. Relative height very variable. Spire callus covering from one half to nearly all of whorl; shape from flat to convex; colour from white, beige, purplish to brown, often darker at upper margin. Callus without distinct colour strokes.

CHANNEL: of medium width.

SUBCHANNEL PATTERN: fasciculated, very variable. Not seen in albinistic, melanistic and in rare, unicoloured specimens.

SHELL BACKGROUND: from white to cream, to yellow, to gray.

COLOUR PATTERN: tents and chevrons of very variable size, width and intensity, sometimes arranged into vertical series. Colour of markings varies from pink to reddish, brown or black. In some populations, markings are diffuse in the direction of growth. The angle of chevrons is large and does not vary appreciably with growth (see Plate 3, fig. 2). Two large spiral bands are formed by local reinforcement of the pattern. Overlay of additional uniform brown colour may cover the whole shell (the so-called "*pattersoni* pattern", see PL. 8, FIG. 6), or may appear in two or more sharply delimited spiral bands (the so-called "*bifasciata* pattern", occurring in widely separated populations, from Colombia to Florida).

COLUMELLA: from nearly smooth, overlaid with thick enamel, to heavily plaited. Colour from white to greyish, to pale purple.

FASCIOLE: mostly uniform white to greyish, base can be suffused with colour. Ridges brown in some populations.

SUPRAFASCIOLAR BAND: very variable.

APERTURE: from white to beige, to faint lilac and greyish blue. Inner margin of lip: variable, from aperture colour to row of darker markings. Aspect depends much on age.

PROTOCONCH: large to extremely large.

Diagnosis. The large values of the protoconch character RES5 and the small NW (number of nuclear volutions) (see Fig. 8, 1-8) set *O. fulgurator* apart from all other *Oliva* species, excepted *O. spicata*. Distinguished from *sayana* by constant angle of chevrons. Distinguished from *O. scripta* by a much narrower channel.

Distribution. Very widely distributed in the Western Atlantic, from Bermudas to Southern Brazil.

SYNONYMY.

O. fulgurator (Röding, 1798), based upon the unambiguous figure 562 of MARTINI (see PL. 6, FIG. 10), is the **valid name** (see TURSCH, DUCHAMPS & GREIFENEDER 1994) for an **objective species** (see § 5.1, 5.4). This is agreement with the conclusions of Z. & P. (1969), W. & A. (1978) and P. & S. (1986). This species is very close (or identical) to the fossil *O. schepmani* Weissbord, 1962 (not treated here).

The following names are synonyms or designate local forms:

Oliva ispida (Link) (not Röding, 1798), 1807. This taxon (being based upon the same figure 562 of MARTINI) is an **objective junior synonym of *O. fulgurator*** (Röding, 1798). It was *O. spicata* (Röding, 1798) for B. & B. (1960); *O. fulgurator* (Röding, 1798) for Z. & P. (1969).

Oliva fusiformis Lamarck, 1811. For original illustration, see PL. 6, FIG. 5. This has been demonstrated (see GREIFENEDER, DUCHAMPS & TURSCH, 1995) to be an **objective junior synonym of *O. fulgurator*** (Röding, 1798), in agreement with B. & B. (1960), Z .& P. (1969), ABBOTT (1974), W. & A. (1978) and P. & S. (1986). It was *O. reticularis* Lamarck, 1811 for DUCROS de St. GERMAIN (1857).

Oliva reticularis Lamarck, 1811. For the availability of this name, see GREIFENEDER, DUCHAMPS & TURSCH (1995). No type material could be located. The original description is:

> "16. Olive réticulaire. ***Oliva reticularis***.
>
> *O. Cylindracea, alba, subbifasciata; lineis fulvis, subpunctatis flexuoso-angulatis; spirâ acutâ.*
>
> Mus., n.12. Encycl., Pl. 361, f. 1.
>
> Martini, Conch. 2, t. 51, f. 561.
>
> Habite... Sur un fond blanc, cette olive offre quantité de lignes en zigzags, rousses, subponctuées. Dans les espaces qu'embrassent deux bandes transverses, ces lignes, plus épaissies et plus colorées, imitent en quelque sorte des caractères d'écriture. Cette olive est peu bombée, a une spire pointue, et ne présente qu'une couleur blanche à son ouverture. Sa longueur est d'environ 45 millimètres. Le bord supérieur du dernier tour est comme dentelé par des taches d'un brun violet, composé de lignes repliées en faisceau."

The illustration in the *Encyclopédie* (Pl. 361, fig. 1, a, b) depicts a specimen inclined at an angle, as evidenced by the aspect of the shoulder, the aperture, and the lower part of the columella. Several other *Oliva* in the *Encyclopédie* are represented in a similar perspective, which, of course, makes a shell appear more globose. So the illustration (see PL. 8, FIG. 9) represents a rather elongated shell, with a peculiar, very concave lip. The large size (45 mm) and the straight sides ("*peu bombée*") indicates that the shell is not the *O. reticularis* of recent authors ("ovate with rounded sides" in P. & S. 1986).

A shell reasonably matching the original illustration has been found in the Récluz collection, at the MHNG, and could possibly be the figured specimen. Shells of this general type are not uncommon in some central Caribbean localities. These forms are linked to the "typical" *O. fulgurator* by an unbroken chain of many intergrading populations. Considerable efforts invested in attempting objective separation, by many different methods and over many years, have always been completely unsuccessful. Much to our regret (for the stability of nomenclature) we are compelled to consider *O. reticularis* Lamarck, 1811 as a local form and a **subjective junior synonym of *O. fulgurator*** (Röding, 1798) (see § 5.1). It was a valid species for Z. & P. (1969), W. & A. (1978) P. & S. (1986) and many other authors.

Oliva olorinella Duclos, 1835. The heterogeneous lot of 8 dirty-white syntypes at MNHN contains specimens of *O. oliva* (L., 1758) (as correctly inferred by KAICHER 1989, who illustrated one such syntype on her card Part IV, no. 5516) as well as shells of Caribbean origin (see PL. 9, FIG. 2). These could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, *Oliva olorinella* Duclos, 1835 (*pars*) is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974), W. & A. (1978) and P. & S. (1986). This name is often utilised to designate a whitish, small form from the Bahamas.

Oliva obesina Duclos, 1840. The type material (figured syntype, out of three, see PL. 6, FIG. 1) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). It is very close to *O. aldinia* Duclos, 1845, and to the semi-fossil *O. schepmani* Weissbord, 1962. Three further specimens have been found in the Duclos collection, at Clermont-Ferrand, under the unpublished name "*O. opisia*". *O. obesina* Duclos, 1840 was *O. spicata* Röding for B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978); a valid species for P. & S. (1986). Shells very similar to the type material are found in Venezuela, in the province of Nueva Esparta.

Oliva timoria Duclos, 1840. The type material is heterogeneous. One of the syntypes (see PL. 7, FIG. 1) is very similar to a brown *O. obesina* Duclos, 1840 (*q.v.*), so *O. timoria* Duclos, 1840 is (*pars*) a **subjective junior synonym of *O. fulgurator*** (Röding, 1798), in agreement with Ducros, 1857 (as *O. reticularis* Lamarck, 1811).

Oliva aldinia Duclos, 1845. The type series (see PL. 6, FIG. 2) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This is in agreement with B. & B. (1960), W. & A. (1978, as "*aldina*", misspelling) and P. & S. (1986). Very similar specimens are found in Venezuela, in the province of Nueva Esparta.

Oliva broderipi Ducros de St. Germain, 1857. The holotype (illustrated by KAICHER 1989, PART IV, card no. 5560, and rightly said not to be *O. oliva*) is very badly worn (see PL. 7, FIG. 3) but nevertheless recognisable shell. It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). It is very close to (if not identical with) *O. (Strephona) contoyensis* Petuch, 1988 (*q.v.*). *O. broderipi* is *O. ispidula* for B. & B. (1960), a colour form of *O. oliva taeniata* Link for P. & S. (1986), a form of *O. oliva* (L., 1758) for Z. & .P (1969) and W. & A.. (1978). *O. broderipi* ; Petuch & Sargent (not Duclos,1857), 1986 (p. 108, Pl. 18, figs. 1, 2) bears no resemblance with the type material and is an *O. oliva* (L., 1758), probably from the Indian Ocean.

Oliva jamaicensis Marrat, 1867. This taxon was re-described in the *Thesaurus*: sp. no. 17, Pl. 4, fig. 26. The holotype (illustrated by KAICHER 1988, Part III, card no. 5187) (see PL. 6, FIG. 6) resembles *O. bewleyi* Marrat, 1870 and could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), *O. scripta* Lamarck, 1811 for ABBOTT (1974), possibly *O. scripta* Lamarck, 1811 for W. & A. (1978) and a valid species for P. & S. (1986).

Oliva oblonga Marrat, 1867. This taxon was re-described in 1870 in the *Thesaurus* (sp. no. 11, Pl. 2, fig. 14). The large holotype (illustrated by KAICHER 1989, Part IV, card no. 5484) (see PL. 6, FIG. 7) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. spicata* (Röding, 1798) for B. & B. (1960), KEEN (1971) and W. & A. (1978); a colour form of *O. tisiphona* Duclos, 1845 for P. & S. (1986) and PETUCH (1987); *O. bewleyi* Marrat, 1870 for DIAZ & PUYANA (1994).

Oliva pallida Marrat, 1867. The taxon was re-described in the *Thesaurus*: 27, sp. no. 138, Pl. 21, figs. 341-343. The type material is missing, as already reported by MCMILLAN (1985). But the identity of the taxon leaves little doubt because Marrat himself considers it as a synonym of his own *O. nivosa* (*q.v.*). His label for the type material of *O. nivosa* Marrat, 1871 reads: "*O. nivosa* 112 Marrat *pallida* Marrat in Annals & Mag. of N. History". In the Index of the *Thesaurus* one also reads: "*pallida* Marr., nivosa, *Marr.*" It follows that *Oliva pallida* Marrat, 1867 is a **local variety of *O. fulgurator*** (Röding, 1798), linked to all other conspecific forms by many intergrading populations. This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and P. & S. (1986); *O. olorinella* Duclos, 1835 for W. & A. (1978). Note: the name *pallida* has been also used by SWAINSON (1831: 78, Pl. 3, fig. 2) for a species of *Agaronia*, by DAUTZENBERG (1910) for a variety of *Oliva flammulata* Lamarck, 1811 and by DAUTZENBERG (1927: 71: 110) for a colour form of *Oliva reticulata* (Röding, 1798).

Oliva bewleyi Marrat, 1870. The holotype (illustrated by KAICHER 1989, Part IV, card no. 5557) (see PL. 7,

FIG. 10) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This is *O. reticularis* Lamarck, 1811 for B. & B. (1960) and W. & A. (1978), a valid species for P. & S. (1986) and DIAZ & PUYANA (1994) who insisted on the extreme variation of this taxon.

Oliva figura Marrat, 1870. The holotype (see PL. 8, FIG. 3) (illustrated by KAICHER 1988, Part III, card no. 5186) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960) and W. & A. (1978). It was a colour form of "*O. jamaicensis brunnea* Marrat" for P. & S. (1986).

Oliva formosa Marrat, 1870. The slim holotype, with several brown spiral stripes (illustrated by KAICHER 1989, Part IV, card no. 5566) (see PL. 9, FIG. 6), could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960) and Z. & P. (1969), a form of the same for ABBOTT (1974), W. & A. (1978) and a colour form of *O. bewleyi* Marrat, 1870 for P & S (1986).

Oliva graphica Marrat, 1870. The swollen, worn holotype (see PL. 6, FIG. 4) (illustrated by KAICHER 1989, Part IV, card no. 5561) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. obesina* Duclos, 1840 for TOMLIN (in FORD 1953); *O. spicata* (Röding, 1798) for B. & B. (1960); *O. scripta* Lamarck, 1811 for OLD (cited in Z & P, 1969), Abbott (1974) and W. & A. (1978); *O. julieta* Duclos, 1840 for Z. & P. (1969) and Keen (1971). It was a valid species for P. & S. (1986: 134, Pl. 23, figs. 7, 8) but their illustration does not at all match the type material.

"***Oliva oblongata*** Marrat, 1870" (auct). This is a misspelling (and a date error) for *O. oblonga* Marrat, 1867 (q.v.). It was *O. spicata* (Röding, 1798) for Z. & P. (1969), W. & A. (1978), Abbott (1974) and P. & S. (1986).

Oliva olivacea Marrat, 1870. This name is available, as *O. olivaceus* Meuschen, 1787 is a nomen nudum (in a rejected work) as noted by W. & A. (1978). The same would apply for *O. olivacea* Karsten, 1789, should the work of that author be rejected by the Commission. Marrat's taxon (illustrated by KAICHER 1988, Part III, card no. 5163), reported as *Oliva olivacea* Meuschen, is certainly a **local variety of *O. fulgurator*** (Röding, 1798), linked to all other conspecific forms by many intergrading populations. It was indeed *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974), W. & A. (1978); *O. bewleyi* Marrat, 1870 for DIAZ & PUYANA (1994). It was a valid species for P & S (1986). Marrat himself wrote "*olivaceus* Meuschen; *reticularis* Lamk." in his caption to Plate IV.

Oliva porcea Marrat, 1870. The very fat holotype (see PL. 6, FIG. 3) is quite similar to *O. obesina* Duclos, 1840, as already stated by TOMLIN (in FORD 1953). It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. spicata* (Röding, 1798) for B. & B. (1960); *O. scripta* Lamarck, 1811 for ABBOTT (1974) and W. & A. (1978); *O. julieta* Duclos, 1840 for Z. & P. (1969) and KEEN (1971).

Oliva hepatica ; Marrat (not Lamarck, 1811), 1871. The shell described in Marrat as *O. hepatica* Lamarck does not correspond to the original, very vague description of Lamarck. Marrat's figures leave little doubt that this is the same as *O. bifasciata* Küster 1878, as already suggested by Z. & P. (1969) and W. & A. (1978). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), possibly a form of the same for Z. & P. (1969), a colour form of *O. tisiphona* Duclos, 1845 for P. & S. (1986). It is in any case a **local variety of *O. fulgurator*** (Röding, 1798). ***O. hepatica*** Lamarck, 1811 is a nomen dubium (see GREIFENEDER, DUCHAMPS & TURSCH 1995).

Oliva bullata Marrat, 1871. The holotype (illustrated by KAICHER 1988, Part III, card no. 5172) (see PL. 9, FIG. 3) is a **local variety of *O. fulgurator*** (Röding, 1798) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. fulgurator* (Röding, 1798) for B. & B. (1960) and W. & A. (1978), a subspecies of the same for P. & S. (1986).

Oliva circinata Marrat, 1871. The holotype (see PL. 9, FIG. 8) (illustrated by KAICHER 1988, Part III, card no. 5526), the four paratypes at MCM, and a probable paratype at AMNH form an homogeneous series that could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. This rather distinctive form very often occupies a peripheral position in scatter diagrams. It also occupies a large, peripheral geographic range all along the coast of Brazil, South of the possible geographical barrier formed by the Amazon River. All populations in this region share the same characteristics, with very little variation save that some (for instance one found in 30 m off Recife) are smaller in size. The temptation to consider this as a subspecies was resisted because extremely similar forms occur in deep water off Florida, in Venezuela and in Colombia. So this taxon is here considered to be a **local variety of *O. fulgurator*** (Röding, 1798). *O. circinata* Marrat, 1871 was *O. sayana* Ravenel, 1834 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and W. & A. (1978); a colour form of *O. graphica* Marrat, 1870 for P. & S. (1986); *O. figura* Marrat, 1870 for DIAZ & PUYANA (1994). *O. circinata* Martyn, 1789, a *nomen nudum* (in a rejected work) was *O. lignaria* Marrat, 1868 for W. & A. (1978).

Oliva mercatoria Marrat, 1871. The two syntypes at MCM (one figured PL. 6, FIG. 9) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was also the interpretation of B. & B. (1960), Z. & .P (1969), W. & A. (1978) and P. & S. (1986).

Oliva nivosa Marrat, 1871. The holotype at MCM (illustrated by KAICHER 1988, Part III, cards no. 5158, 5159) (see PL. 7, FIG. 9) and one possible paratype could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & .P (1969), ABBOTT (1974) and W. & A. (1978); a valid species for P. & S. (1986).

Oliva reclusa Marrat, 1871. The holotype (see PL. 9, FIG. 7), illustrated as "syntype" by KAICHER 1988, Part III, (card no. 5247) was correctly described by TOMLIN (in FORD 1953) as "a pale *reticularis* Lam. It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). Very similar specimens are found in Aruba (see HEMMEN 1981). This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and W. & A. (1978); a valid species for P. & S. (1986) and PETUCH (1987).

Oliva bifasciata Küster in Weinkauff, 1878. The locality given is "South coast of America (Marrat), probably Brazil and Guyana". The reference "Pl. 10, figs. 8,9" in the text is wrong and is corrected to " Pl. 10, Figs. 10, 11" in the "Erklärung der Tafeln". The figured specimen (H: 61.39 mm, D: 26.73 mm) (see PL. 8, FIG. 4) SMF no. 9353 represents a striking, but common colour variant, encountered in many Caribbean populations. It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as a **colour form of *O. fulgurator*** (Röding, 1798). *O. bifasciata* Küster in Weinkauff, 1878 was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974), W. & A. (1978); a separate, valid species for P. & S. (1986).

Oliva cribraria Marrat, 1883? This taxon is represented by a properly labelled holotype in MCM. The work in which the publication appeared is unknown. According to MCMILLAN (1985) "Description and col. fig. of this species exist in print (two copies); possibly ex Marrat's privately printed *Notebook of a Liverpool Naturalist* (1833)". The upper edge of the fasciole of the beautiful holotype (see PL. 9, FIG. 10) is delimited by a thin, bright purple zone (more vivid than in *O. circinata* Marrat, 1871, to which the shell is very closely related). The type (with a purple protoconch) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). Locality unknown. This was *O. oblonga* Marrat for TOMLIN in FORD (1953).

Oliva reticularis bollingi Clench, 1934. The heavy holotype (see PL. 7, FIG. 8) (illustrated by KAICHER 1989, Part IV, card no. 5543) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). *O. bollingi* Clench, 1934 was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and W. & A. (1978); a subspecies of *O. bifasciata* Küster, 1878 for P. & S. (1986). This form comes from crab traps, off Miami, Florida.

Oliva reticularis greenwayae Clench, 1937. The holotype (see PL. 8, FIG. 5) (illustrated by KAICHER 1989, Part IV, card no. 5562) is extremely similar to the figured specimen of *O. bifasciata* Küster in Weinkauff, 1878 (see PL. 8, FIG. 4). It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety** (and colour form) **of *O. fulgurator*** (Röding, 1798). *O. reticularis greenwayae* Clench, 1937 was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969) and ABBOTT (1974); *O. bifasciata* Küster, 1878 for W & A (1978) and P. & S. (1986). This form comes from Smith Point, Grand Bahama Island, Bahamas.

Oliva reticularis pattersoni, Clench, 1945. The dark, heavy holotype (see PL. 8, FIG. 6) (illustrated by KAICHER 1989, Part IV, card no. 5568) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety** (and colour form) **of *O. fulgurator*** (Röding, 1798). *O. pattersoni* Clench, 1945 was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969) and ABBOTT (1974); *O. formosa* Marrat, 1870 for W. & A. (1978) and KAICHER (1989); a colour form of *O. bifasciata bollingi* Clench, 1937 (sic) for P. & S. (1986). This form comes from 5 miles E of Crabbing Point, Great Bahama Island, Bahamas.

Oliva drangai Schwengel, 1951. The light-coloured holotype (see PL. 7, FIG. 7) (previously illustrated by KAICHER 1988, Part III, card no. 5165, as "*O. drangae*") could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). *O. drangai* Schwengel, 1951 was probably *O. scripta* Lamarck, 1811 for W. & A .(1978); a valid species for P. & S. (1986). This form comes from Pigeon Pt., Tobago. Note: the holotype (ANSP 247107) has an abnormal, tilted protoconch. The protoconch of the smaller (H: 18.56 mm; D: 8.46 mm) paratype (ANSP 247093) is normal.

Oliva antillensis Petuch & Sargent, 1986. The holotype (see PL. 9, FIG. 1) (illustrated by KAICHER 1988, Part III, card no. 5245) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form comes from the Southern coast of Gonave Island, HAITI. This was *O. bewleyi* Marrat for DIAZ & PUYANA (1994).

Oliva bahamasensis Petuch & Sargent, 1986. The holotype (see PL. 8, FIG. 10) (illustrated by KAICHER 1989, Part IV, 5575) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was caught in a lobster pot, in 200 m off Grand Bahama I.

Oliva barbadensis Petuch & Sargent, 1986. The holotype (see PL. 9, FIG. 4) (illustrated by KAICHER 1989, Part IV, card no. 5531) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form comes from deep water (200 m) off St. James, Barbados. Other deep water specimens from close neighbouring localities have a very different colour pattern.

Oliva bifasciata jenseni Petuch & Sargent, 1986. The holotype (see PL. 7, FIG. 6) (illustrated by KAICHER 1988, Part III, card no. 5202) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was collected in shallow water (0.5 m), in Bermuda.

Oliva finlayi Petuch & Sargent, 1986. The holotype (see PL. 8, FIG. 8) (illustrated by KAICHER 1988, Part III, card no. 5184) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This is a deep water form, from 200 m, Matanzas Bay, Cuba.

Oliva goajira Petuch & Sargent, 1986. The holotype (see PL. 8, FIG. 2) (illustrated by KAICHER, 1988, Part III, card no. 5189) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form comes from 60 m off Cabo La Vela, Colombia. It falls within the range of variation of *O. circinata* Marrat, 1871 for DIAZ & PUYANA (1994). An extremely similar form lives in 5-6 m, coarse sand, Tayrona, Colombia.

Oliva jamaicensis zombia Petuch & Sargent, 1986. The holotype (see PL. 7, FIG. 2) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was collected on sand flats, Southern side of Gonave I., Haiti.

Oliva magdae Petuch & Sargent, 1986. The holotype (see PL. 6, FIG. 8) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was caught in a fish trap, 300 m, off Matanzas Bay, Cuba.

Oliva maya Petuch & Sargent, 1986. The holotype (see PL. 8, FIG. 1) (illustrated by KAICHER 5186) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was trawled by a shrimper in 35 m. off Contoy Is., Yucatan, Mexico. It is broadly sympatric with *Oliva contoyensis* Petuch, 1988, but there is no clear indication that the two taxa are syntopic. For reasons unknown to us, *O. maya* was considered by PETUCH & SARGENT (1986: 121) to belong to their "*sayana* group".

Oliva bifasciata sunderlandi Petuch, 1987. The holotype (see PL. 9, FIG. 5) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was trawled from 150 m West of Cedar Key, Florida.

Oliva circinata tostesi Petuch, 1987. The holotype (see PL. 9, FIG. 9) (illustrated by KAICHER 1989, Part IV, card no. 5530) and several topotypes could not be separated from a large sample of *O. fulgurator circinata* Marrat, 1871, encompassing several populations. This, being described from a single population, does hardly qualify as a subspecies and is (at best) a **local variety of *O. fulgurator*** (Röding, 1798).

Oliva sargenti Petuch, 1987. The holotype (see PL. 7, FIG. 5) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was collected in 5 m, Malmok, Aruba.

Oliva contoyensis Petuch, 1988. The holotype (see PL. 7, FIG. 4) is very similar to that of *O. broderipi* Ducros de St. Germain, 1857 (*q.v.*). It could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was collected in 35 m. off Contoy I., Yucatan, Mexico. It is broadly sympatric with *Oliva maya* Petuch & Sargent, 1986, but there is no clear indication that the two taxa are syntopic.

Oliva ernesti Petuch 1990. The holotype (see PL. 8, FIG. 7) could not be separated from the "*fulgurator-reticularis* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. fulgurator*** (Röding, 1798). This form was trawled in 40 m, silty sand, off Portobello, Panama (East Coast).

The following names have been mistakenly (or very questionably) considered as synonyms:

Oliva oriola ; Duclos (not Lamarck, 1811), 1835: Pl. 10, figs. 1, 2, text in *Illustr. Conch.*: 15. This was *O. spicata* (Röding, 1798) and *O. reticularis* Lamarck, 1811 for W & A (1978). It was *O. spicata* (Röding, 1798) for B. & B. (1960), Z. & P. (1969) and KEEN (1971). Duclos' illustrations of *O. oriola* Lamarck, 1811 are somewhat ambiguous and, in the absence of specimens in the Duclos collection, attribution is most uncertain. It would be better to consider this as a **nomen dubium**. In any case, this is a junior homonym of *O. oriola* Lamarck, 1811 (see GREIFENEDER, DUCHAMPS & TURSCH 1995).

Oliva quersolina Duclos, 1835: Pl. 10, figs.7-8. This is *O. olorinella* Duclos, 1835 for W. & A. (1978) and *O. reticularis* Lamarck, 1811 for Z. & P. (1969), ABBOTT (1974) and P. & S. (1986). *O. quersolina* has been demonstrated to be a **subjective junior synonym** of the Indian Ocean species *O. atalina* Duclos, 1835 (see TURSCH & GREIFENEDER 1996).

Oliva memnonia Duclos, 1845: 15, Pl. 17, figs. 19-20. This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and W. & A .(1978). The original figures (illustrated by KAICHER 1989, Part IV, card no. 5497) are not recognisable with any certainty. In the absence of type material, it is much safer to consider this name as a **nomen dubium**.

Oliva tisiphona Duclos, 1845. No type material has been located. The characteristic sub-channel pattern of the "*fulgurator-reticularis* complex" is not apparent on the illustrations of DUCLOS and is not mentioned in the original description. Although DUCLOS says this taxon is rather close to *O. oniska* Duclos, 1845, his illustrations are quite problematic and it is certainly safer to consider this as a **nomen dubium**. This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974) and W. & A .(1978). P. & S. (1986) consider this to be a valid species, but it is not at all evident that the specimen they illustrate (Pl. 29, figs. 11-12) matches the original figure.

"***Oliva alba*** Lamarck" was listed, without a word of clarification, by GRAY (1858: 44) in the synonymy of *Strephona reticularis*. This is a **misquotation**, as there is no *O. alba* Lamarck (see GREIFENEDER, DUCHAMPS & TURSCH 1995). Gray refers to sp. no. 42 (*O. candida*) of Lamarck for which "*alba*" is part of the Latin description (see B. & B. 1960).

"***Oliva vermiculata*** Lamarck" was listed, without a word of clarification, by GRAY (1858: 44) in the synonymy of *Strephona reticularis*. This is a **misquotation**, as there is no *O. vermiculata* Lamarck (see GREIFENEDER, DUCHAMPS & TURSCH 1995).

"*Oliva diaphana* Duclos 1835" (auct.) was *O. reticularis* Lam. for B & B (1960), W & A (1978) and P. & S. (1986). This is a **misquotation**, as there is no *Oliva diaphana* described by Duclos.

"***Oliva vermiculata*** Gray, 1858" (auct.) constitutes a fine example of sequential taxonomic hallucinations in the genus *Oliva*. This non-existent taxon was *O. reticularis* Lamarck, 1811 for B. & B. (1960) and W. & A. (1978). It was considered to be a valid species by P. & S. (1986: 155). PETUCH (1987: 105) even described an *Oliva* from Haiti as "closely resembling Gray's type of *O. vermiculata*". One wonders where this type material could be seen. "*Oliva vermiculata* Gray, 1858" is a **misquotation** because there is no *O. vermiculata* Gray. One finds a citation of "*vermiculata* Lamarck" in Gray (1858: 44), in the synonymy of *Strephona reticularis*). But this is yet another misquotation, as there is no such thing as a "*O. vermiculata* Lamarck" (*q.v.*).

Oliva sowerbyi Marrat, 1870: 13, sp. no. 61, Pl. 8, figs. 114,115. This was *O. reticularis* Lamarck, 1811 for B. & B. (1960), Z. & P. (1969), ABBOTT (1974), W. & A. (1978) and P. & S. (1986). *Oliva sowerbyi* Marrat, 1870 (not illustrated here) has been demonstrated to be a **subjective junior synonym** of the very different Indian Ocean species ***O. atalina*** Duclos, 1835 (see TURSCH & GREIFENEDER, 1996). *Oliva sowerbyi* Anton, 1839: 102 is does not to the genus *Oliva* but is a small fossil, possibly an *Ancilla*. (see TURSCH & GREIFENEDER, 1996). Likewise, *Oliva sowerbyi* Ducros de St-Germain, 1857: 105, sp. no. 103 is not an *Oliva* but an *Olivella*.

Oliva polpasta Duclos, 1833.

Oliva polpasta Duclos, 1833: Pl. 20; 1840: Pl. 16, figs. 1-2; 1844: 26.

Oliva truncata Marrat, 1867: 215.
Oliva kerstitchi da Motta, 1985: 8-9.
Oliva olssoni Petuch & Sargent, 1986: 140, Pl. 25, figs. 17, 18.

Description.

SIZE: to over 50 mm.

SHAPE: ovate to biconic.

SPIRE: flat conical. Spire callus covers from 1/2 to nearly all the whorl. Colour of callus from bluish grey to yellow, beige and brown, often darker in upper zone; occasional dark strokes or points.

CHANNEL: medium.

SUBCHANNEL PATTERN: fasciculated, forming a regular, narrow zone of black triangles pointing upwards alternating with whitish triangles of equal size, pointing downwards. When seen in apical view, this produces a characteristic "cogwheel pattern" (see PL. 3, FIG. 6).

SHELL BACKGROUND: yellowish brown to olive gray to bluish gray.

COLOUR PATTERN: network of chevrons of variable thickness (mostly blurred to produce nearly homogeneous backdrop), overlaid with a pattern of single dark blotches, sometimes forming strokes, chevrons or ziczacs. Two faint large spiral bands (not always present) are formed by local reinforcement of the pattern. Some specimens have one or two wide spiral white bands ("*kerstitchi* pattern").

COLUMELLA: rather smooth, mostly white, with very faint yellow to green shadow only at the base.

FASCIOLE: uniform white.

SUPRAFASCIOLAR BAND: lower part often with nearly axial, sharp strokelets.

APERTURE: white to pale greyish or yellowish. Inner margin of lip: like aperture; dark brown or grey only in shells with a sharp lip.

PROTOCONCH: medium large.

Diagnosis. Differs from *O. spicata* by the all-white fasciole, the "cogwheel pattern" (see PL. 3, FIG. 6) and a protoconch generally smaller.

SYNONYMY.

Oliva polpasta Duclos, 1833. This taxon (of which the figured syntype is illustrated PL. 4, FIG. 6), although closely related to *O. spicata* (Röding, 1798), is easily and totally separated from that species (see TURSCH & HUART, 1990) by quantitative characters. Both are syntopic (for instance at Cebaco I., Panama) and *Oliva polpasta* Duclos, 1833 thus is the **valid name** for a separate, **objective species**, in agreement with Z. & P. (1969), W. & A. (1978) and P. & S. (1986). It was a variety of *O. spicata* (Röding, 1798) for B. & B. (1960). This species is very close (or identical) to the fossils *O. davisae* Durham, 1950 and *O. callosa* Li, 1930 (not treated here).

The following names are synonyms or designate local forms:

Oliva truncata Marrat, 1867. The holotype (see PL. 4, FIG. 7) could not be separated from *O. polpasta* Duclos, 1833. In the absence of valid arguments to the contrary, this is here considered as a **subjective junior synonym of *O. polpasta*** Duclos, 1833. This was a valid species for P. & S. (1986). It was *O. elegans* Lamarck, 1811 (a completely different Indo-Pacific species, see GREIFENEDER, DUCHAMPS & TURSCH 1995) for B. & B. (1960) Z. & P. (1969) and W. & A. (1978).

Oliva kerstitchi da Motta, 1985. The holotype (see PL. 4, FIG. 8) (with the label "*kirstitchi*") could not be separated from *O. polpasta* Duclos, 1833, except for the presence of a white spiral band on the body whorl. TURSCH & HUART (1990) considered this as having specific status, as a working hypothesis, awaiting further confirmation (see § 1.1.3). Further work (see § 4.1) established that *O. kerstitchi* da Motta, 1985 is consistently syntopic with *O. polpasta* Duclos, 1833, to which it is linked by an unbroken chain of intergrades (KOCH 1992). In the absence of valid arguments to the contrary, this is here considered as a **colour form of *O. polpasta*** Duclos, 1833. This was a valid species for P. & S. (1986).

Oliva olssoni Petuch & Sargent, 1986. The faded, bulging holotype (see PL. 4, FIG. 9) presents the characteristic sub-channel "cogwheel pattern" and could not be separated from *O. polpasta* Duclos, 1833, to which it is linked by an unbroken chain of intergrades (bulging forms of *O. polpasta* are not uncommon, for instance in Panama). In the absence of valid arguments to the contrary, this is here considered as a **local variety of *O. polpasta*** Duclos, 1833.

Oliva sayana Ravenel, 1834.

Oliva sayana Ravenel, 1834: 19.

- *Oliva litterata* Lamarck (not Röding, 1798), 1811: 315, sp. no. 20.
- *Oliva circinata* var. *citrina* Johnson, 1911: 23.
- *Oliva (Strephona) sayana sarasotensis* Petuch & Sargent, 1986: 146, Pl. 28, figs. 4, 5.
- *Oliva (Strephona) sayana texana* Petuch & Sargent, 1986: 147, Pl. 38, figs. 3, 4.

Description.

SIZE: to over 70 mm.

SHAPE: elongated fusiform to cylindrical. In old specimens, anterior part of lower lip very heavy and extended outwards.

SPIRE: conical and distinctly telescopic. Spire callus covering only 1/3 or 1/2 of the whorl. Colour of callus beige or gray to orange, with no markings.

CHANNEL: medium.

SUBCHANNEL PATTERN: coarsely fasciculated, very rapidly shifting to tent pattern.

SHELL BACKGROUND: whitish-grey to yellow.

COLOUR PATTERN: tents and chevrons of variable size, sometimes arranged into vertical series. Very large white tents are common. Two large spiral bands are formed by local reinforcement of the pattern. The angle of chevrons starts small and does appreciably increase with growth (see PL. 3, FIG. 1). Golden forms occur, with overall yellow appearance and reduction of the pattern.

COLUMELLA: with very strong coarse plaits, often smoothed by enamel. Colour white.

SUPRAFASCIOLAR BAND: very variable.

APERTURE: inner part often lilac to pink, changing to whitish grey or cream towards the lip. Inner margin of lip: dark (interrupted or not) in shells with sharp lip.

PROTOCONCH: small.

Diagnosis. Differs from *O. fulgurator* and *O. scripta* by a marked increase of the angle of chevrons during growth (see PL. 3, FIGS. 1, 2), a much smaller protoconch, a telescopic spire. Differs from *O. scripta* by a much narrower channel.

Distribution. Southeastern coast ud U.S. and Gulf of Mexico. According to P. & S. (1986: 121), *O. sayana* "cannot tolerate the tropical carbonate environment of the southern tip of Florida ... [which] acts as a barrier to dispersal"

SYNONYMY.

Oliva sayana Ravenel, 1834. The type is missing in the Ravenel collection, housed at the Charleston Museum (*fide* Dr. Harry D. LEE, *in litt*). There is no original figure, nor any actual description. Comparing this shell to *O. litterata* (described by Lamarck as being 66 to 68 mm -about 2.75 inches- long), Ravenel writes:

> "These Shells are certainly distinct, and therefore should be distinguished by different names. The O. sayana, sometimes exceeds 3 inches in length –fine specimens are rare– worn specimens are not uncommon on the coast of South Carolina."

With so little information, this widely used name should normally be a *nomen dubium*. Nomenclatural stability can nevertheless be preserved by an unusual (but good) argument: no other *Oliva* species is found on the coast of South Carolina (a very intensively prospected area). This species is easily and completely separated by quantitative criteria from all other Atlantic *Oliva* species (see TURSCH & HUART,1990), so one can consider that *Oliva sayana* Ravenel, 1834 is the **valid name** for an **objective species**, in agreement with Z. & P. (1969), W. & A. (1978) and P. & S. (1986).

The following names are synonyms or designate local forms:

Oliva litterata Lamarck, 1811. This (see original illustration PL. 5, FIG. 1) is the former name of *O. sayana* Ravenel, 1834, in agreement with B. & B. (1960), Z. & P. (1969), W. & A. (1978) and .P & S. (1986). It is a **junior homonym of *O. litterata*** (Röding, 1798) (see TURSCH & al., 1994), a synonym of *O. spicata* (Röding, 1798) for KEEN (1971), a nomen dubium for TURSCH, DUCHAMPS & GREIFENEDER, 1994.

Oliva circinata* var. *citrina Johnson, 1911. Examination of the paratype MCZ 6267 (figured here PL. 5, FIG. 4) (illustrated by KAICHER 1989, Part IV, card no. 5482) confirms this is a **colour form of *O. sayana*** Ravenel, 1834, in agreement with B. & B. (1960), Z. & P. (1969), W. & A. (1978) and .P & S. (1986). This conclusion is supported by the characteristic small, intact protoconch.

Oliva sayana sarasotensis Petuch & Sargent, 1986. The rather small (40 mm) holotype (see PL. 5, FIG. 3) (previously illustrated by KAICHER 1989, Part IV, card no. 5493) could not be separated from a large sample of *O. sayana* Ravenel, 1834, containing many populations. This, being described from a single population (15 km West of Lido Beach, Sarasota, Florida), does hardly qualify as a subspecies. In the absence of valid arguments to the contrary, it is here considered as a **local variety of *O. sayana*** Ravenel, 1834.

Oliva sayana texana Petuch & Sargent, 1986. The holotype (see PL. 5, FIG. 2) (previously illustrated by KAICHER 1989, Part IV, card no. 5487) could not be separated from a large sample of *O. sayana* Ravenel, 1834, containing many populations. This, being described from a single population (shallow water, Padre I., off South Texas), does hardly qualify as a subspecies. In the absence of valid arguments to the contrary, it is here considered as a **local variety of *O. sayana*** Ravenel, 1834.

The following names have been mistakenly considered as synonyms:

Oliva polita Marrat, 1867. The two small, dark syntypes (with no locality data) at MCM (one illustrated by Kaicher 1988, Part III, card no. 5190) do not at all resemble *O. sayana* Ravenel, 1834 and are most probably the Polynesian form of *O panniculata* Duclos, 1835, an extremely different, well-known Indo-Pacific shell. This was *O. sayana* Ravenel, 1834 for B. & B. (1960), Z. & P. (1969) and ABBOTT (1974).

Oliva circinata Marrat, 1871 (*q.v.*, under *O. fulgurator*) was *O. sayana* Ravenel, 1834 for ABBOTT (1974).

Oliva scripta Lamarck, 1811.

Oliva scripta Lamarck, 1811: 315, sp. no. 21; *Encycl.* Pl. 362, fig .4.

Oliva caribaeensis Dall & Simpson, 1901: 391, Pl. 56, fig. 9.

Oliva trujilloi Clench, 1938: 109-113, Pl. 9.

Oliva (Cariboliva) scripta venezuelana Petuch & Sargent, 1986: 71, Pl. 4, figs. 20, 21.

SIZE: to over 50 mm.

SHAPE: cylindrical.

SPIRE: low conical, telescopic. Spire callus semi-convex to convex, covering from half to whole whorl. Colour beige, without ornamentation.

CHANNEL: extremely wide.

SUBCHANNEL PATTERN: fasciculated, variable.

SHELL BACKGROUND: pale beige, occasionally whitish.

COLOUR PATTERN: network of fine strokes, forming tents and triangles of variable size. This is overlaid by fine dark brown markings sometimes arranged in axial series, concentrated in two spiral bands. These often contain long fine strokes or chevrons. Near the shoulder, the angle of these dark chevrons coincides with that of the fine strokes pattern. In many specimens, the angle of the fine strokes pattern becomes progressively larger as one goes towards the base, while the angle of the dark chevrons remains nearly constant (see PL. 3, FIG. 3).

COLUMELLA: mostly with coarse plaits over all the length, often with white enamel.

FASCIOLE: white to faint beige.

SUPRAFASCIOLAR BAND: lower zone with parallel fine strokes of variable shape; upper zone with parallel, axial strokes.

APERTURE: greyish white, sometimes faint purplish, rarely violet. Inner lip margin dark in specimens with sharp lip.

PROTOCONCH: medium large.

Diagnosis. Readily distinguished from all other *Oliva* species by its extremely wide channel.

Distribution: From Florida to Brazil.

SYNONYMY.

Oliva scripta Lamarck, 1811. As for all Lamarck's *Oliva* species, the type material could not be located. The original figure is reproduced in PL. 5, FIG. 5. *O. scripta* Lamarck, 1811 is the **valid name** (see GREIFENEDER, DUCHAMPS & TURSCH 1995) of an **objective species** (see TURSCH & HUART 1990), in agreement with the conclusions of ABBOTT (1974) and P. & S. (1986). This name has been applied by Z. & P. (1969) and W. & A. (1978) to another species with an Indo-Pacific distribution.

The following names are synonyms or designate local forms:

Oliva caribaeensis Dall & Simpson, 1901. The holotype (see PL. 5, FIG. 6) (previously illustrated by KAICHER 1989, Part IV, card no. 5526) could in no way be distinguished from *O. scripta* Lamarck, 1811, of which it is a **subjective junior synonym**. This is in agreement with the conclusions of W. & A. (1978), OLD (cited in Z. & P. 1969), ABBOTT (1974) and DIAZ & PUYANO (1994). It was a valid species for Z. & P. (1969), who state that in Puerto Rico, solid color intergrades link this taxon with *O. reticularis* Lamarck, 1811 –not confirmed on the solid coloured Portorican specimens examined by us.

Oliva trujilloi Clench, 1938. The holotype (see PL. 5, FIG. 7) (previously illustrated by KAICHER 1988, Part III, card no. 5200) and the six paratypes examined (see PL. 5, FIG. 8 and FIG. 9) are dead shells that could not be distinguished from *O. scripta* Lamarck, 1811 except for their reddish colouration, commonly seen in old shells that have been long exposed to sunlight. *O. trujilloi* Clench, 1938 is a **subjective junior synonym of *O. scripta*** Lamarck, 1811, in agreement with the conclusions of B. & B. (1960, as *O. caribaeensis*), W. & A. (1978), OLD cited in Z. & P. (1969), ABBOTT (1974), P. & S. (1986) and DIAZ & PUYANO (1994).

Oliva scripta venezuelana Petuch & Sargent, 1986. The holotype (see PL. 5, FIG. 10) (previously illustrated by KAICHER 1988, Part III, card no. 5199) is linked by an unbroken series of intergrading specimens (Shells with very similar, nebulose colour pattern are found in Honduras) to other populations of *O. scripta* Lamarck, 1811. It is, at best, a **local form of *O. scripta*** Lamarck, 1811, in agreement with the conclusions of DIAZ & PUYANO (1994).

The following names have been mistakenly or questionably considered as synonyms:

Oliva leucostoma d'Orbigny, 1842 (belonging to the genus *Olivancillaria* according to B. & B., 1960) was considered by W. & A. (1978) to be a probable synonym of *O. scripta* Lamarck, 1811. Even if *O. leucostoma* d'Orbigny, 1842 belonged to the genus *Oliva*, it would be a younger homonym of *O. leucostoma* Duclos, 1840.

Oliva jamaicensis Marrat, 1867, [a local variety of *O. fulgurator* (Röding, 1798)] was considered by Z. & P. (1969) to be a possible synonym, and by ABBOTT (1974) to be a synonym of *O. caribaeensis* Dall & Simpson, 1901.

Oliva graphica Marrat, 1870 [a local variety of *O. fulgurator* (Röding, 1798)] was considered by ABBOTT (1974) to be a possible synonym of *O. scripta* Lamarck, 1811.

Oliva porcea Marrat, 1870 [a local variety of *O. fulgurator* (Röding, 1798)] was considered by ABBOTT (1974) to be a possible synonym of *O. scripta* Lamarck, 1811.

Oliva spicata (Röding, 1798).

Porphyria spicata Röding, 1798: 35, sp. no. 423.

- *Porphyria arachnoidea* (Röding, 1798): 36, sp. no. 450.
- *Oliva araneosa* Lamarck, 1811: 315, sp. no. 19.
- *Oliva venulata* Lamarck, 1811: 313, sp. no. 13; *Encycl.* Pl. 361, fig. 5.
- *Oliva oniska* Duclos, 1845: 19, Pl. 32, figs. 7-9.
- *Oliva pindarina* Duclos, 1840: Pl. 16, figs. 7-8; 1845: 19.
- *Oliva timoria* Duclos, 1840: Pl. 17, figs. 11-13; *Illustr. Conch.*: 19 (*pars*).
- *Oliva subangulata* Philippi, 1848: Pl. 1, fig. 2.
- *Oliva cumingii* Reeve, 1850: Pl. 11, figs. 19, a, b.
- *Oliva ligneola* Reeve, 1850: sp. no. 57, Pl. 21, fig. 57.
- *Oliva melchersi* Menke, 1851: 24.
- *Oliva intertincta* Carpenter, 1857: 465.
- *Oliva violacea* Marrat, 1867: 213.
- *Oliva brunnea* Marrat, 1870: 7, sp. no. 24, figs. 54, 55.
- *Oliva punctata* Marrat, 1870: sp. n° 6, Pl.2, figs. 12-13.
- *Oliva fuscata* Marrat, 1870: sp. n° 8, figs. 20-22.
- *Oliva spicata* var. *hemphilli* Ford in Johnson, 1911: 122.
- *Oliva spicata* var. *perfecta* Johnson, 1911: 122.
- *Oliva rejecta* Burch & Burch, 1962: 165.
- *Oliva ionopsis* Berry, 1969: 163-64.
- *Oliva (Strephona) radix* Petuch & Sargent, 1986: 143, Pl.26, figs.20-23.
- *Oliva subangulata corteziana* Petuch & Sargent, 1986: 150, Pl. 29, figs. 7-10.

Description.
Local populations are very homogeneous. The ranges of variations here under describe differences *between* populations.

SIZE: from about 25 mm to over 65 mm.

SHAPE: very variable, from elongated fusiform to inflated fusiform. Cylindrical forms do not seem to occur. Strong tendency to inflated, angular shoulders (biconical appearance).

SPIRE: conical, rather elevated. Spire callus rarely covering more than half of whorl, colour from white, beige, purplish to brown, often darker at upper margin. Callus often presents oblique dark strokes.

CHANNEL: of medium width.

SUBCHANNEL PATTERN: fasciculated, very variable. Not seen in albinistic, melanistic and in unicoloured specimens.

SHELL BACKGROUND: from white to cream, to yellow, to gray.

COLOUR PATTERN: tents and chevrons of very variable size, width and intensity. Colour of markings varies from reddish to brown or black. Start of chevrons often marked with small blotch. Two faint large spiral bands are formed by local reinforcement of the pattern. Some populations are nearly devoid of colour pattern and have overall golden or whitish appearance. Overlay of additional uniform brown colour often covers the whole shell, but the Caribbean "*bifasciata* pattern" is absent (or very rare).

COLUMELLA: very variable. Colour from white to greyish, to pale purple.

FASCIOLE: mostly uniform white to greyish, purplish or brownish. Lower part often suffused with colour. Ridges often marked with light brown to dark purplish brown.

SUPRAFASCIOLAR BAND: very variable.

APERTURE: from white to beige, to greyish blue and purple. Inner margin of lip: variable, from aperture colour to continuous or interrupted darker markings.

PROTOCONCH: large to very large.

Diagnosis. The large values of the protoconch character RES5 and the small NW (number of nuclear volutions) (see Fig. 8, 11-18) set *O. spicata* (Röding, 1798) apart from all other *Oliva* species, excepted *O. fulgurator* (Röding, 1798). In most cases, it differs from *O. fulgurator* (Röding, 1798) by much weaker spiral bands, (the Caribbean "*bifasciata* pattern" is absent or very rare), by the presence of oblique strokes on the spire callus and by the presence of coloured fasciolar ridges.

Distribution. Widely distributed in the Panamic region, from the Gulf of California to Ecuador.

SYNONYMY.

Oliva spicata (Röding, 1798), based upon the acceptable figures 509 and 510 of MARTINI (see PL. 10, FIG. 5), is the **valid name** (see TURSCH, DUCHAMPS & GREIFENEDER 1994) for an **objective species** (see § 4.1) . This is agreement with the conclusions of Z. & P. (1969), W. & A .(1978), P. & S. (1986) and. For a colour variation see JACKSON (1991).

The following names are synonyms or designate local forms:

"***Oliva arachmoidea***" (Röding, 1798) in W. & A. (1978) is a **printing error** for *O. arachnoidea* (Röding, 1798) (*q.v.).*

Oliva arachnoidea (Röding, 1798) is an **objective junior synonym of *O. spicata*** (Röding, 1798) (see TURSCH, DUCHAMPS & GREIFENEDER 1994), in agreement with B. & B. (1960), Z. & .P (1969), KEEN (1971), ABBOTT (1974), W. & A. (1978) and P. & S. (1986).

Oliva araneosa Lamarck, 1811. This is an **objective junior synonym of *O. spicata*** (Röding, 1798) (see TURSCH, DUCHAMPS & GREIFENEDER 1994), in agreement with B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974), W. & A. (1978) and P. & S. (1986). It was a colour form of the same for TERZER (1996).

"***Oliva aranersa*** Lamarck, 1811" (auct) in W. & A. (1978) is a **printing error** for *O. araneosa* Lamarck, 1811.

Oliva venulata Lamarck, 1811. This is an **objective junior synonym of *O. litterata*** (Röding, 1798) (see GREIFENEDER, DUCHAMPS & TURSCH 1995), which is itself a nomen dubium (see TURSCH, DUCHAMPS & GREIFENEDER 1994). This was a valid species for DUCLOS (1845: 25; Pl. 17, figs. 5, 6; Pl. 22, figs. 19, 20; Pl. 33, fig.11, illustrating rather dissimilar shells) and for P. & S. (1986). It was a form of *O. spicata* (Röding, 1798) for B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). It was a separate species for TERZER (1996).

Oliva timoria Duclos, 1840. The type material is heterogeneous. One of the syntypes (see PL. 10, FIG. 1) is very similar to *O. radix* Petuch & Sargent, 1986, so *O. timoria* Duclos, 1840 is (*pars*) a **subjective junior synonym** of ***O. spicata*** (Röding, 1798).

"***Oliva onisca*** Duclos, 1844" (auct) is a **misspelling** for *O. oniska* Duclos, 1845. This was *O. fulgurator* (Röding, 1798) for B. & B. (1960).

Oliva oniska Duclos, 1845. The type series consists in 6 mottled specimens and 3 brown specimens, including the figured syntype (see PL. 11, FIG. 4) (illustrated by KAICHER 1989, Part IV, card no. 5473). The type material could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as a **subjective junior synonym of *O. spicata*** (Röding, 1798), in agreement with Z. & P. (1969). This was *O. fulgurator* (Röding, 1798) for W. & A. (1978); a subspecies of *O. tisiphona* Duclos, 1845 (a nomen dubium) for P. & S. (1986).

Oliva pindarina Duclos, 1840. The type material, including the figured syntype (see PL. 10, FIG. 2) (illustrated by KAICHER 1989, Part IV, card no. 5523), could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as a **local form of *O. spicata*** (Röding, 1798), in agreement with B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). This was a colour form of *O. venulata* Lamarck, 1811 for P. & S. (1986) and for TERZER (1996). Similar to some forms of *O. fulgurator*

Oliva subangulata Philippi, 1848. This is represented in BM(NH) by two specimens, with the label "type" fallen off. One of the specimens bears traces of glue and is most probably the holotype. This shell (see PL. 11, FIG. 6), with a slight shoulder bulge, could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as a **local form of *O. spicata*** (Röding, 1798), in agreement with Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). This was a valid species for P. & S. (1986) and for TERZER (1996).

Oliva cumingii Reeve, 1850. The three syntypes (see PL. 11, FIG. 1) (one is illustrated by KAICHER 1989, Part IV, card no. 5551) with the label "Gulf of California. H. Cuming colln." have a banded colour pattern and are somewhat bulging. The type material could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). It was a subspecies of *O. venulata* Lamarck, 1811 for P. & S. (1986); a form of the same for TERZER (1996).

Oliva ligneola Reeve, 1850. One of the two heterogeneous syntypes (see PL. 10, FIG. 3) is a specimen of *O. tigrina fallax* Johnson, 1910, for which *ligneola* Reeve, 1850 would thus be an earlier name. The other one is a bleached shell that could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, *O. ligneola* Reeve, 1850 (*pars*) is here considered as yet another **subjective junior synonym of *O. spicata*** (Röding, 1798). This was a nomen dubium for W. & A. (1978).

Oliva melchersi Menke, 1851. There is no type material and no original illustration. The original description says that the shell is angular, ash and flesh in colour, with yellowish ("*ochroleucus*"), triangular blotches and brown dots. The shoulder presents a pattern of lines in bundles("American pattern"). Lower whorls of spire uniformly flesh coloured, with brown spots above; lip sharp, with black maculations. The above description, together with the type locality (Mazatlan, Mexico) and the mention by the author that it could be a freak of *O. venulata* Lamarck, 1811, indicates this is a **subjective junior synonym** of ***O. spicata*** (Röding, 1798), in agreement with B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974), and W. & A. (1978). It was a subspecies of *O. spicata* (Röding, 1798) for P. & S. (1986) and for TERZER (1996).

Oliva intertincta Carpenter, 1857. The two homogeneous syntypes USNM 716187 (see PL. 11, FIG. 9) are dead, discoloured, juvenile specimens of *O. spicata* (Röding, 1798). So are the three additional syntypes at BM(NH) (see KEEN 1968). All have a brown fasciole and the second whorl of the protoconch is more inflated than usual, both characters intergrading with *O. spicata* (Röding, 1798), of which this is here considered to be a **subjective junior synonym**. This is in agreement with the conclusions of B & B (1960), Z & P (1969), KEEN (1971) ABBOTT (1974) W & A (1978), P & S (1986) and TERZER (1996).

Oliva violacea Marrat, 1867. The holotype (see PL. 11, FIG. 8) (illustrated by KAICHER 1989, Part IV, card no. 5479) could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with B. & B. (1960), KEEN (1971), ABBOTT (1974), Z. & P. (1969) and W. & A. (1978). This was a valid species for TERZER (1996) and for P. & S. (1986), but *O. violacea* ; Petuch & Sargent (not Marrat, 1867), 1986, depicted in the *Atlas*, Pl. 30, figs. 20, 21 differs very much from the type specimen.

Oliva brunnea Marrat, 1870. The brown holotype (see PL. 11, FIG. 3) (illustrated by KAICHER 1989, Part IV, card no. 5573) is nearly identical to one of the syntypes of *Oliva fuscata* Marrat, 1870 (*q.v.*, see PL. 11, FIG. 2). It could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety** (and colour form) **of *O. spicata*** (Röding, 1798), in agreement with B. & B. (1960) and W. & A. (1978). It was a subspecies of the Atlantic taxon *O. jamaicensis* Marrat, 1870 for P. & S. (1986). This taxon is indeed one of the cases of striking resemblance between populations of *O. fulgurator* (Röding, 1798) and populations of *O. spicata* (Röding, 1798) (see § 5.4). Some specimens from Paranagua, Venezuela are extremely similar to their Pacific counterparts.

Oliva punctata Marrat, 1870. This name is available because *O. punctata* (Röding, 1798) is a nomen nudum (see TURSCH, DUCHAMPS & GREIFENEDER 1994). According to TOMLIN (in FORD, 1953) the 8 specimens at MCM are not types because the largest specimen (said to be 33 mm x 16 mm) is not large enough. But according to MCMILLAN (1985), the two syntypes are the originals of Marrat's figures. In any case, these specimens (see PL. 10, FIG. 4) could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with Z. & P. (1969), KEEN (1971) and ABBOTT (1974). This was *O. spicata* var. *venulata* Lamarck, 1811 for B. & B. (1960); *O. rejecta* Burch & Burch, 1962 for P. & S. (1986) and for TERZER (1996). "*punctulata* Johnson, 1911" is a misquotation in B & B (1960) and W & A (1978) for *punctata* Marrat, cited in Johnson (1911: 122) under *spicata*.

Oliva fuscata Marrat, 1870. The type material consists of three syntypes [Note: TOMLIN (in FORD, 1953) mentions six syntypes]. Two are mottled (one is figured PL. 11, FIG. 7); the last (see PL. 11, FIG. 2) is brown and nearly identical with the type of *O. brunnea* Marrat, 1870. The type material could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974), W. & A. (1978), P. & S. (1986) and TERZER (1996).

Oliva spicata* var. *hemphilli Ford in Johnson, 1911. The five syntypes (see PL. 10, FIG. 8) could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978). This was a colour form of *O. venulata* Lamarck, 1811 for P. & S. (1986) and for TERZER (1996).

Oliva spicata* var. *perfecta Johnson, 1911. The three homogeneous, dark syntypes (the largest is figured here PL. 11, FIG. 5) could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **colour form of *O. spicata*** (Röding, 1798), in agreement with B. & B. (1960), Z. & P. (1969) and KEEN (1971). This was *O. fuscata* Marrat, 1870 for W. & A. (1978); *O. venulata* Lamarck, 1811 for P & S (1986) and TERZER (1996).

Oliva rejecta Burch & Burch, 1962 is a specially interesting case, as this is the only report known to us of syntopic coexistence of two forms within the "*spicata* complex" (an information contradicted by recent field observations, see § 4.3.2). The examined paratypes at USNM (see PL. 10, FIG. 10) (illustrated by KAICHER 1989, Part IV, card no. 5527)and MNHN (see PL. 10, FIG. 9) could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. The reported differences -base of columella light purple instead of white, D/H 0.42 (calculated from reported measurements of two specimens only; 0.43 measured on paratypes) instead of 0.49- fall well within the variation range of the "*spicata* complex". The other reported difference -brittleness of the shell, making it unsuitable for producing Indian artifacts- and reported differences in the X-Ray diffraction pattern of the shell (DONOHUE & HARDCASTLE 1962) could not be tested by us, as this would entail destruction of type material. These could certainly represent interpopulation variation. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with the conclusions of Z & P (1969) KEEN (1971) ABBOTT (1974). It was a valid species (*Oliva punctata* Marrat, 1870) for P. & S. (1986) and for TERZER (1996). This form comes from La Paz, Baja California, Mexico, on tide flats.

Oliva ionopsis Berry, 1969: 163-64. The holotype (see PL. 11, FIG. 10) (previously illustrated in HERTZ (1984: 37, Fig. 89) and the seven paratypes could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. For instance, the blue aperture (to which the name refers) is also found in the varieties *violacea* Marrat, 1867, *rejecta* Burch and Burch, 1962 as well as in many unnamed forms. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798), in agreement with KEEN (1971) and TERZER (1996). It was considered a valid species by ABBOTT (1974), W. & A. (1978) and P. & S. (1986). The type locality is Bahia de las Palmas, Baja California, in 10-33 fms.

Oliva radix Petuch & Sargent, 1986. The holotype (see PL. 10, FIG. 6) (previously illustrated by KAICHER 1989, Part IV, card no. 5486) has an angulose shape that somewhat reminds of some bulgy forms of *O. polpasta* Duclos (a species broadly co-occurring in Ecuador, see KEEN, 1971) but lacks the characteristic subchannel "cogwheel" pattern of this species (see under *O. polpasta*). Shells of *O. spicata* (Röding, 1798) with rather similar shapes (but less bulgy) occur in Western Mexico. The protoconch measurements (RES5= 1.58, NW=2.50, see Fig. 3) and (PAT18/NW = 0.4, lpro = 0.82, see Fig. 6) also indicate it is a **local variety of *O. spicata*** (Röding, 1798).

Oliva subangulata corteziana Petuch & Sargent, 1986. In spite of its more bulging body whorl (see **PL. 10, FIG. 7**), the holotype could not be separated from the "*spicata* complex" morphological continuum, being linked to all other conspecific forms by many intergrading populations. In the absence of valid arguments to the contrary, this is here considered as yet another **local variety of *O. spicata*** (Röding, 1798). This form comes from the Northern end of the Gulf of California. This was a valid subspecies of *O. subangulata* Philippi, 1848 for TERZER (1996).

The following names have been mistakenly (or very questionably) considered as synonyms:

Oliva harpularia Lamarck, 1811 is a nomen dubium (see GREIFENEDER, DUCHAMPS & TURSCH 1995). This was *O. spicata* (Röding, 1798) for B. & B. (1960) and W. & A. (1978); a colour form of *O. venulata* Lamarck,1811 for P. & S. (1986); a possible synonym of *O. pindarina* Duclos, "1835" for TERZER (1996).

Oliva ustulata Lamarck, 1811 is another nomen dubium (see GREIFENEDER, DUCHAMPS & TURSCH 1995). This was a synonym of *O. reticularis* Lamarck, 1811 for DUCLOS (1845, p. 16); *O. spicata* (Röding, 1798) for B. & B. (1960); a form of *O. spicata* (Röding, 1798) for Z. & P. (1969); possibly *O. fuscata* Marrat, 1870 for W. & A. (1978); a colour form of *O. venulata* Lamarck,1811 for P. & S. (1986) and for TERZER (1996).

Oliva oriola ; Duclos (not Lamarck, 1811), 1835: Pl. 10, figs. 1, 2, text in *Illustr. Conch.*: 15. This was *O. spicata* (Röding, 1798) for B. & B. (1960), Z. & P. (1969), KEEN (1971) , ABBOTT (1974) and W. & A. (1978). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

Oliva obesina Duclos, 1840. This was *O. spicata* Röding for B. & B. (1960), Z. & P. (1969), KEEN (1971), ABBOTT (1974) and W. & A. (1978); a separate Panamic species for TERZER (1996). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

Oliva ispida (Link) (not Röding, 1798), 1807. This was *O. spicata* (Röding, 1798) for B. & B. (1960). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

Oliva oblonga Marrat, 1867. This was *O. spicata* (Röding, 1798) for B. & B. (1960), KEEN (1971) and W. & A. (1978). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

Oliva graphica Marrat, 1870. This was *O. spicata* (Röding, 1798) for B. & B. (1960). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

"***Oliva oblongata*** Marrat, 1870" (auct). This was *O. spicata* (Röding, 1798) for Z. & P. (1969), W. & A. (1978), ABBOTT (1974) and P. & S. (1986). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

Oliva porcea Marrat, 1870. This was *O. spicata* (Röding, 1798) for B. & B. (1960). This name has already been treated under *O. fulgurator* (Röding, 1798) (*q.v.*).

One name is still unsolved:

Oliva schumacheriana Beck in Gray (1858: 46) (original name: *Strephona schumacheriana*), cited by B. & B. (1960) as "Beck 1858 Cal. Proc. 1858, p.46") could not be tracked. The only indication in Gray is "Front of pillar lip brown. *Hab.* California". This possibly refers to the ridges of the fasciole, often marked with brown in *O. spicata* (Röding, 1798).

Oliva spicata deynzerae Petuch & Sargent, 1986.

Oliva (Strephona) spicata deynzerae Petuch & Sargent, 1986: 149, Pl. 28, figs. 12, 13.

Description.

SIZE: to over 55 mm.

SHAPE: elongated fusiform.

SPIRE: conical, slightly telescopic. Spire callus gray brown to purple, covering up to 2/3 of whorl, with dark brown oblique strokes.

CHANNEL: medium.

SUBCHANNEL PATTERN: fasciculated, of variable intensity.

SHELL BACKGROUND: whitish.

COLOUR PATTERN: Network of fine tent marks (giving bluish-gray aspect) is overlaid with dark brown little blotches, especially concentrated to form two large spiral bands, in which are found strokes, chevrons and ziczacs.

COLUMELLA: with sharp plaits over all the length. Colour purplish white.

FASCIOLE: same colour as columella, with smoky base and upper margin purple.

SUPRAFASCIOLAR BAND: two similar zones of puncticulated brown marks.

APERTURE: beige-cream.

PROTOCONCH: medium large.

Diagnosis. Spire more telescopic than *O. spicata*. Double spiral band more conspicuous.

Distribution. Known only from the Cocos Islands, Costa Rica.

Oliva spicata deynzerae Petuch & Sargent, 1986. The holotype (see PL. 4, FIG. 5) and the six topotypes that were examined could be separated from all the remainder of the "*O. spicata* complex" (see § 5. 3 and Fig. 18). This is therefore considered as a **subspecies of *Oliva spicata*** (Röding, 1798), in agreement with P. & S. (1986) and TERZER (1996). All specimens examined had a very similar colour pattern, curiously reminiscent of that of the sympatric species *Oliva foxi* Stingley, 1984 (local crypsis pattern?). The subspecies status rests on a rather small sample (see § 5. 3) and would have to be modified if another form of *O. spicata* were to be discovered in the Cocos Is.

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8. INDEX TO NAMES (objective species in **bold**)

"*alba* Lamarck": misquotation in Gray (1858).

"*aldina*" Duclos: misspelling for *O. aldinia* Duclos, 1845.

aldinia Duclos, 1845: subjective junior synonym of *O. fulgurator* (Röding, 1798).

angulata Lamarck, 1811: objective junior synonym of *O. incrassata* (Röding, 1798).

antillensis Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

" *arachmoidea*" (Röding, 1798) (auct.): printing error for *O. arachnoidea* (Röding, 1798).

arachnoidea (Röding, 1798): objective junior synonym of *O. spicata* (Röding, 1798).

araneosa Lamarck, 1811: objective junior synonym of *O. spicata* (Röding, 1798).

"*aranersa*" Lamarck, 1811 (auct.): printing error for *O. araneosa* Lamarck, 1811.

bahamasensis Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

barbadensis Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

bewleyi Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

bifasciata Küster in Weinkauff, 1878: colour form of *O. fulgurator* (Röding, 1798).

bifasciata jenseni Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

bifasciata sunderlandi Petuch, 1987: local variety of *O. fulgurator* (Röding, 1798).

bollingi Clench, 1934: see *reticularis bollingi* Clench, 1934.

broderipi Ducros de St.Germain, 1857: local variety of *O. fulgurator* (Röding, 1798).

brunnea Marrat, 1870: local variety of *O. spicata* (Röding, 1798).

bullata Marrat, 1871: local variety of *O. fulgurator* (Röding, 1798).

caribaeensis Dall & Simpson, 1901: subjective junior synonym of *O. scripta* Lamarck, 1811.

circinata Martyn, 1789:*nomen nudum* (in a rejected work).

circinata Marrat, 1871: local variety of *O. fulgurator* (Röding, 1798).

circinata var. *citrina* Johnson, 1911: colour form of *O. sayana* Ravenel, 1834.

circinata tostesi Petuch, 1987: local variety of *O. fulgurator* (Röding, 1798).

citrina Johnson, 1911: see *circinata* var. *citrina* Johnson, 1911

contoyensis Petuch, 1988: local variety of *O. fulgurator* (Röding, 1798).

corteziana Petuch & Sargent, 1986: see *subangulata corteziana* Petuch & Sargent, 1986.

cribraria Marrat, 1833? : local variety of *O. fulgurator* (Röding, 1798).

cumingii Reeve, 1850: local variety of *O. spicata* (Röding, 1798).

deynzerae Petuch & Sargent, 1986: see *spicata deynzerae*.

"*diaphana* Duclos 1835" (auct.): misquotation.

drangai Schwengel, 1951: local variety of *O. fulgurator* (Röding, 1798).

ernesti Petuch 1990: local variety of *O. fulgurator* (Röding, 1798).

figura Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

finlayi Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

formosa Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

foxi Stingley, 1984: valid.

fulgurator (Röding, 1798): valid.

fuscata Marrat, 1870: local variety of *O. spicata* (Röding, 1798).

fusiformis Lamarck, 1811: objective junior synonym of *O. fulgurator* (Röding, 1798).

goajira Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

graphica Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

greenwayae Clench, 1937: see *reticularis greenwayae* Clench, 1937.

harpularia Lamarck, 1811: nomen dubium.

hemphilli Ford in Johnson, 1911: see *spicata* var. *hemphilli* Ford in Johnson, 1911.

hepatica ; Marrat (not Lamarck, 1811), 1871: local variety of *O. fulgurator* (Röding, 1798).

incrassata (Lightfoot in Solander, 1786): valid.

ionopsis Berry, 1969: local variety of *O. spicata* (Röding, 1798).

intertincta Carpenter, 1857: subjective junior synonym of *O. spicata* (Röding, 1798)

ispida (Link) (not Röding, 1798), 1807: objective junior synonym of *O. fulgurator* (Röding, 1798).

jamaicensis Marrat, 1867: local variety of *O. fulgurator* (Röding, 1798).

jamaicensis zombia Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

jenseni Petuch & Sargent, 1986: see *bifasciata jenseni* Petuch & Sargent, 1986.

kerstitchi da Motta, 1985: colour form of *O. polpasta* Duclos, 1833.

ligneola Reeve, 1850 (*pars*): subjective junior synonym of *O. spicata* (Röding, 1798); (pars): earlier name for *tigrina fallax* Johnson, 1910.

litterata (Röding, 1798): nomen dubium.

litterata Lamarck, 1811: junior homonym of *O. litterata* (Röding, 1798).

magdae Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

maya Petuch & Sargent, 1986: local variety of *O. fulgurator* (Röding, 1798).

melchersi Menke, 1851: subjective junior synonym of *O. spicata* (Röding, 1798).

memnonia Duclos, 1845: nomen dubium.

mercatoria Marrat, 1871: local variety of *O. fulgurator* (Röding, 1798).

nivosa Marrat, 1871: local variety of *O. fulgurator* (Röding, 1798).

obesina Duclos, 1840: local variety of *O. fulgurator* (Röding, 1798).

oblonga Marrat, 1867: local variety of *O. fulgurator* (Röding, 1798).

"*oblongata* Marrat, 1870" (auct): misspelling (and a date error) for *O. oblonga* Marrat, 1867.

olivacea Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

olorinella Duclos, 1835 (*pars*): local variety of *O. fulgurator* (Röding, 1798).

olorinella Duclos, 1835 (*pars*): subjective junior synonym of *O. oliva* (L., 1758).

olssoni Petuch & Sargent, 1986: local variety of *O. polpasta* Duclos, 1833.

"*onisca* Duclos, 1844" (auct): misspelling for *O. oniska* Duclos, 1845.

oniska Duclos, 1845: subjective junior synonym of *O. spicata* (Röding, 1798).

oriola ; Duclos (not Lamarck, 1811), 1835: nomen dubium.

pallida Marrat, 1867: local variety of *O. fulgurator* (Röding, 1798).

pattersoni, Clench, 1945 4: local form and colour variety of *O. fulgurator* (Röding, 1798).

perfecta Johnson, 1911: see *spicata* var. *perfecta* Johnson, 1911.

pindarina Duclos, 1840: local variety of *O. spicata* (Röding, 1798).

polpasta Duclos, 1833: valid.

porcea Marrat, 1870: local variety of *O. fulgurator* (Röding, 1798).

punctata (Röding, 1798): nomen nudum.

punctata Marrat, 1870: local variety of *O. spicata* (Röding, 1798).

"*punctulata* Johnson, 1911" (auct.): misquotation.

quersolina Duclos, 1835: subjective junior synonym of *O. atalina* Duclos, 1835.

radix Petuch & Sargent, 1986: local variety of *O. spicata* (Röding, 1798).

reclusa Marrat, 1871: local variety of *O. fulgurator* (Röding, 1798).

rejecta Burch & Burch, 1962: local variety of *O. spicata* (Röding, 1798).

reticularis Lamarck, 1811: subjective junior synonym of *O. fulgurator* (Röding, 1798).

reticularis bollingi Clench, 1934: local variety of *O. fulgurator* (Röding, 1798).

reticularis greenwayae Clench, 1937: local form and colour variety of *O. fulgurator* (Röding, 1798).

sarasotensis Petuch & Sargent, 1986: see *sayana sarasotensis* Petuch & Sargent, 1986.

sargenti Petuch, 1987: local variety of *O. fulgurator* (Röding, 1798).

sayana Ravenel, 1834: valid.

sayana sarasotensis Petuch & Sargent, 1986: local form of *O. sayana* Ravenel, 1834.

sayana texana Petuch & Sargent, 1986: local form of *O. sayana* Ravenel, 1834.

schumacheriana Beck in Gray (1858): unknown to us, possibly *O. spicata* (Röding, 1798).

scripta Lamarck, 1811: valid.

scripta venezuelana Petuch & Sargent, 1986: local form of *O. scripta* Lamarck, 1811.

sowerbyi Marrat, 1870: subjective junior synonym of *O. atalina* Duclos, 1835.

spicata (Röding, 1798): valid.

spicata deynzerae Petuch & Sargent, 1986: subspecies of *O. spicata* (Röding, 1798).

spicata var. *hemphilli* Ford in Johnson, 1911: local variety of *O. spicata* (Röding, 1798).

spicata var. *perfecta* Johnson, 1911: colour form of *O. spicata* (Röding, 1798).

subangulata Philippi, 1848: local variety of *O. spicata* (Röding, 1798).

subangulata corteziana Petuch & Sargent, 1986: local variety of *O. spicata* (Röding, 1798).

sunderlandi Petuch, 1987: see *bifasciata sunderlandi* Petuch, 1987.

texana Petuch & Sargent, 1986: see *sayana texana* Petuch & Sargent, 1986.

timoria Duclos, 1840 (*pars*): subjective junior synonym of *O. fulgurator* (Röding, 1798).

timoria Duclos, 1840 (*pars*): subjective junior synonym of *O. spicata* (Röding, 1798).

tisiphona Duclos, 1845: nomen dubium.

tostesi Petuch, 1987: see *circinata tostesi* Petuch, 1987.

trujilloi Clench, 1938: subjective junior synonym of *O. scripta* Lamarck, 1811.

truncata Marrat, 1867: subjective junior synonym of *O. polpasta* Duclos, 1833.

ustulata Lamarck, 1811: nomen dubium.

venezuelana Petuch & Sargent, 1986: see *scripta venezuelana* Petuch & Sargent, 1986.

venulata Lamarck, 1811: objective junior synonym of *O. litterata* (Röding, 1798).

"*vermiculata* Gray, 1858" (auct.): misquotation and nomen nudum.

"*vermiculata* Lamarck": misquotation in Gray (1858).

violacea Marrat, 1867: local variety of *O. spicata* (Röding, 1798).

zombia Petuch & Sargent, 1986: see *jamaicensis zombia* Petuch & Sargent, 1986.

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PLATE 1.

Examples of subchannel colour pattern in Atlantic and Eastern Pacific *Oliva* species (see text § 4.1).

1. *O. foxi* Stingley, 1984. Cocos Is., Costa Rica.
2. *O. foxi* Stingley, 1984. Cocos Is., Costa Rica.
3. *O. porphyria* (Linnaeus, 1758). W. Mexico.
4. *O. porphyria* (Linnaeus, 1758). Cebaco I., W. Panama.
5. *O. polpasta* Duclos, 1833. Kobbe Beach, W. Panama.
6. *O. polpasta* Duclos, 1833. Montijo Bay, W. Panama.
7. *O. incrassata* (Lightfoot in Solander, 1786). Baja California, W. Mexico.
8. *O. incrassata* (Lightfoot in Solander, 1786). Baja California, W. Mexico.
9. *O. julieta* Duclos, 1840. Gubernadora I., W. Mexico.
10. *O. julieta* Duclos, 1840. Manzanillo, W. Mexico.
11. *O. splendidula* Sowerby, 1825. W. Panama.
12. *O. splendidula* Sowerby, 1825. W. Panama.
13. *O. spicata* (Röding, 1798). Baja California, W. Mexico.
14. *O. spicata* (Röding, 1798). Baja California, W. Mexico.
15. *O. sayana* Ravenel, 1834. Marco Beach, Florida, USA.
16. *O. sayana* Ravenel, 1834. Morgans Pass, Florida, USA.
17. *O. scripta* Lamarck, 1811. Honduras.
18. *O. scripta* Lamarck, 1811. Honduras.
19. *O. fulgurator* (Röding, 1798) f. *reticularis* Lamarck, 1811. E. Panama.
20. *O. fulgurator* (Röding, 1798). Aruba.
21. *O. fulgurator* (Röding, 1798) f. *circinata* Marrat, 1871. Ilha Bela, Brazil.
22. *O. fulgurator* (Röding, 1798) f. *circinata* Marrat, 1871. Salvador, Brazil.
23. *O. spicata deynzerae* Petuch & Sargent, 1986. Cocos Is., Costa Rica.
24. *O. spicata deynzerae* Petuch & Sargent, 1986. Cocos Is., Costa Rica.
25. *O. kaleontina* Duclos, 1835. Melon I., W. Panama.
26. *O. kaleontina* Duclos, 1835. Cebaco I., W. Panama.
27. *O. undatella* Lamarck, 1811. W. Mexico.
28. *O. undatella* Lamarck, 1811. San Pedro, Ecuador.
29. *O. peruviana* Lamarck, 1811. Iquique, Chile.
30. *O. peruviana* Lamarck, 1811. Iquique, Chile.
31. *O. flammulata* Lamarck, 1811. Luanda, Angola.
32. *O. flammulata* Lamarck, 1811. La Awera, Mauritania.
33. *O. flammulata dolicha* Locard, 1896. São Vicente, Cabo Verde.
34. *O. flammulata dolicha* Locard, 1896. São Vicente, Cabo Verde.

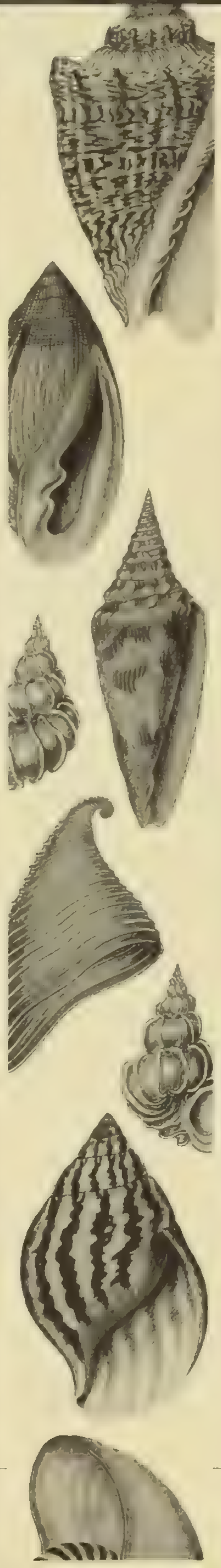
ERRATUM

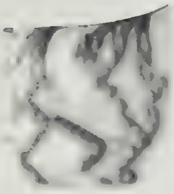
APEX, Vol. 12(4), 20 décembre 1997

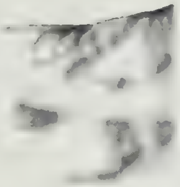
Description d'une nouvelle espèce de Costellariidae des Philippines, par E. Guillot de Suduiraut.

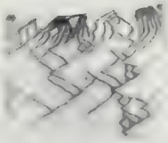
Page 119 : lire *Vexillum (Costellaria) sauternesense* n. sp. au lieu de *V. (C.) sauternesi* n. sp.

Page 119 : read *Vexillum (Costellaria) sauternesense* n. sp. instead of *V. (C.) sauternesi* n. sp.

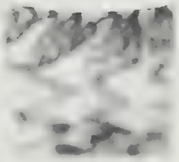


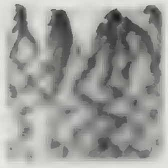

1. *O. foxi*


2. *O. foxi*

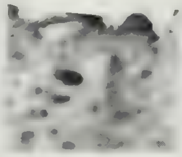

3. *O. porphyria*


4. *O. porphyria*


5. *O. polpasta*

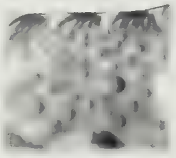

6. *O. polpasta*

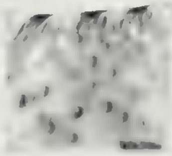

7. *O. incrassata*


8. *O. incrassata*

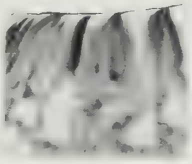

9. *O. julieta*


10. *O. julieta*

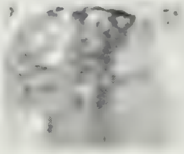

11. *O. splendidula*


12. *O. splendidula*

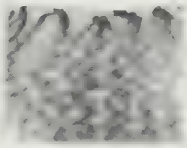

13. *O. spicata*

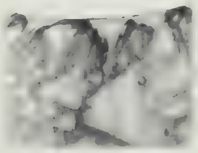

14. *O. spicata*


15. *O. sayana*


16. *O. sayana*

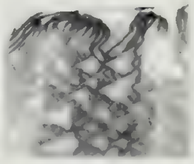

17. *O. scripta*

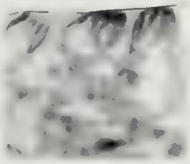

18. *O. scripta*


19. *O. fulgurator*
f. *reticularis*


20. *O. fulgurator*

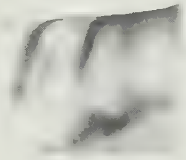

21. *O. fulgurator*
f. *circinata*


22. *O. fulgurator*
f. *circinata*


23. *O. spicata*
deynzerae

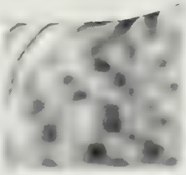

24. *O. spicata*
deynzerae

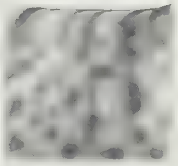

25. *O. kaleontina*


26. *O. kaleontina*


27. *O. undatella*

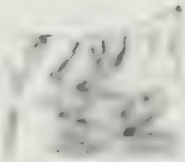

28. *O. undatella*


29. *O. peruviana*


30. *O. peruviana*


31. *O. flammulata*


32. *O. flammulata*


33. *O. flammulata*
dolicha


34. *O. flammulata*
dolicha

PLATE 2.

An example of occurrence of distinct, conspecific *Oliva* populations in neighbouring localities.

O. spicata (Röding, 1798) in the vicinity of La Paz, Baja California, Mexico.

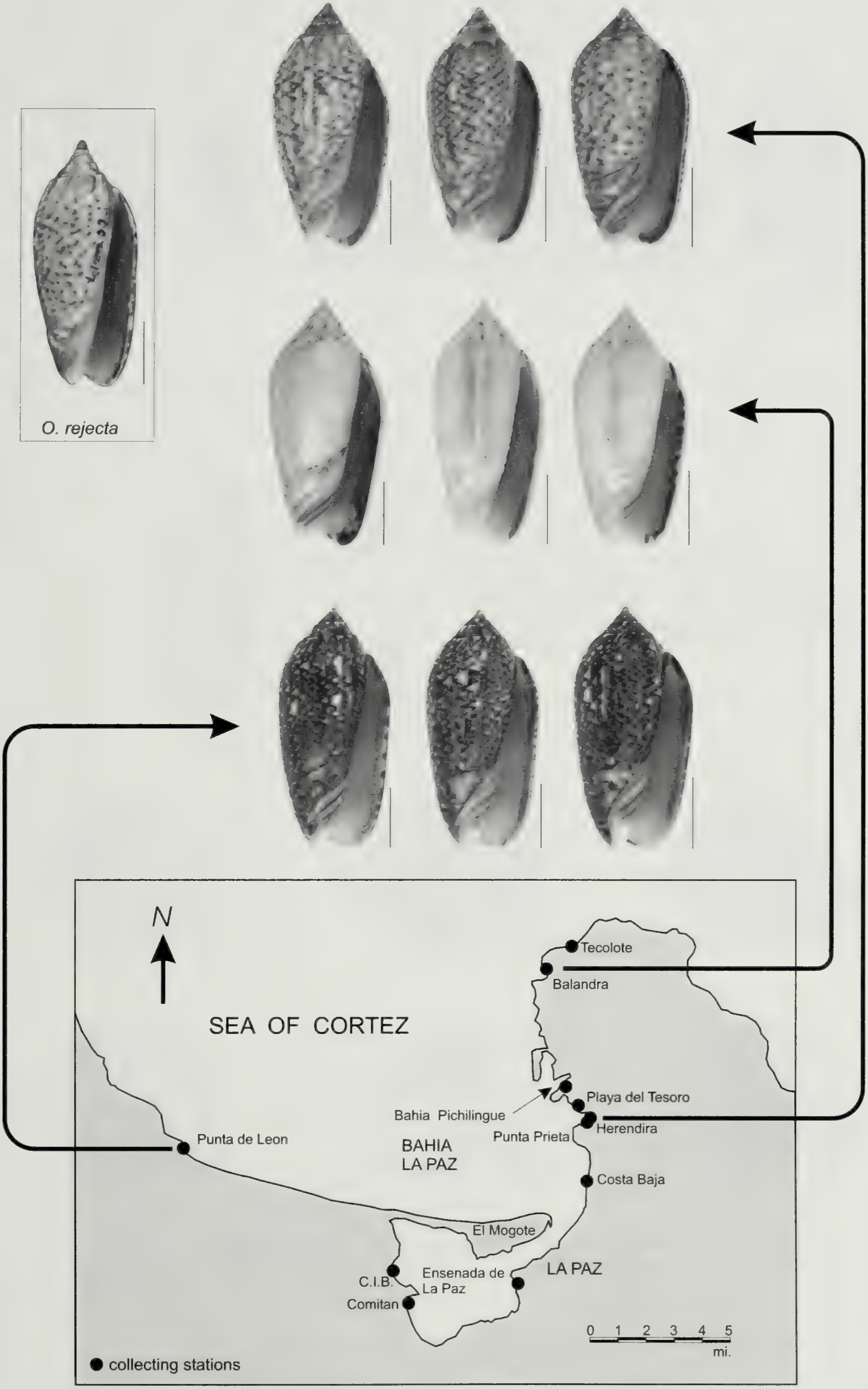
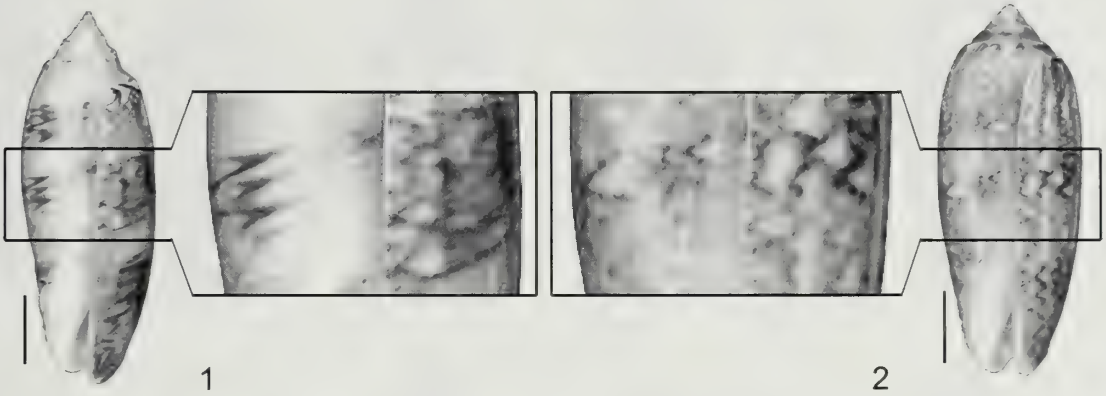

O. rejecta
N
SEA OF CORTEZ
Tecolote
Balandra
Bahia Pichilingue
Playa del Tesoro
Herendira
Punta Prieta
Punta de Leon
BAHIA
LA PAZ
Costa Baja
El Mogote
LA PAZ
Ensenada de
La Paz
C.I.B.
Comitan
0 1 2 3 4 5
mi.
● collecting stations

PLATE 3.

Some tips for quick identification.



Figs. 1-2. Tip for quick identification of *O. sayana* (**1**). The angle of chevrons increases markedly during growth, while in *O. fulgurator* (**2**) the angle of chevrons stays nearly constant. Scale bars: 10 mm.

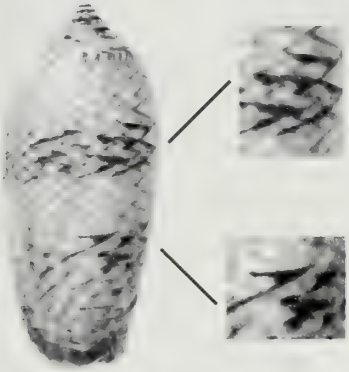
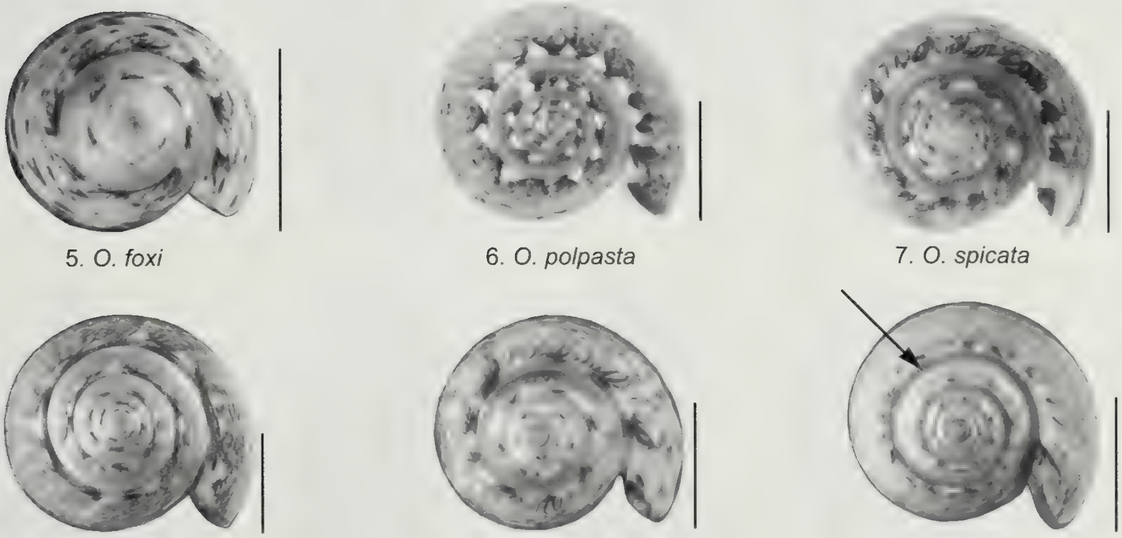


Fig. 3. Tip for quick identification of *O. scripta*. In most specimens, the angle of the fine strokes pattern becomes progressively larger as one goes towards the base, while the angle of the dark chevrons remains nearly constant



5. *O. foxi*
6. *O. polpasta*
7. *O. spicata*
8. *O. sayana*
9. *O. fulgurator*
10. *O. scripta*

Figs. 4-10. Tip for quick identification of *O. polpasta* (**6**): characteristic "cogwheel pattern" in apical view, very rarely present in other related species. Note the very wide filament channel of *O. scripta* (**10**). Scale bars: 10 mm.

PLATE 4. Type material.

1-4. ***O. foxi*** Stingley, 1984.

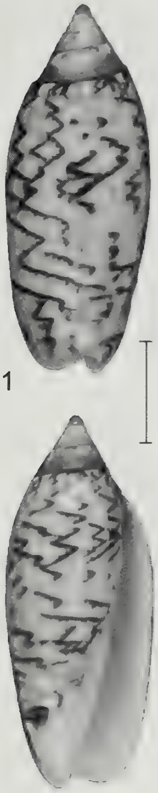
1. HOLOTYPE ANSP 358356. (H: 36.98 mm, D: 14.82 mm). Cocos I., COSTA RICA.
2. PARATYPE ANSP 358357. (H: 37.60 mm, D: 15.17 mm). Cocos I., COSTA RICA.
3. PARATYPE AMNH 264800. (H: 34.9 mm, D: 14.1 mm). COCOS Is., COSTA RICA.
4. PARATYPE AMS C.170890. (H: 33.35 mm; D: 13.36 mm). COCOS Is., COSTA RICA. .

5. ***O. spicata deynzerae*** Petuch & Sargent, 1986.

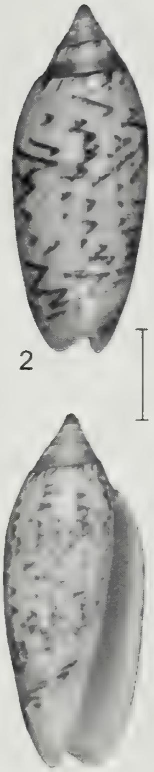
5. HOLOTYPE USNM 841452 (H: 53.19 mm; D: 21.95 mm). COCOS Is., COSTA RICA.

6-9. ***O. polpasta*** Duclos, 1833.

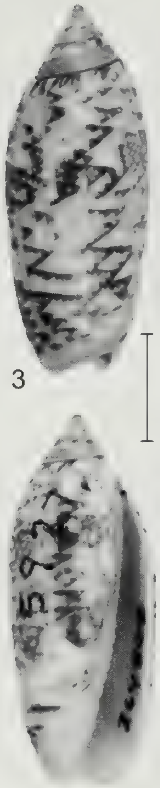
6. *O. polpasta* Duclos, 1833. FIGURED SYNTYPE, MNHN (H: 40.1 mm; D: 21.0 mm).
7. *O. truncata* Marrat, 1867. HOLOTYPE, MCM (H: 37 mm, D: 18 mm).
8. *O. kerstitchi* da Motta, 1985. HOLOTYPE MHNG 984.631 (H: 24.5, D: 11.2 mm).
9. *O. olssoni* Petuch & Sargent, 1986. Holotype USNM 841444 (H: 35.03 mm; D: 19.57 mm). 60 m off Gulf of Panama (8°7'N, 78°40'W), PANAMA.


1

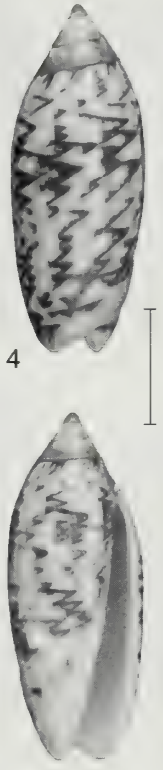
O. foxi


2

O. foxi
par. ANSP


3

O. foxi
par. AMNH


4

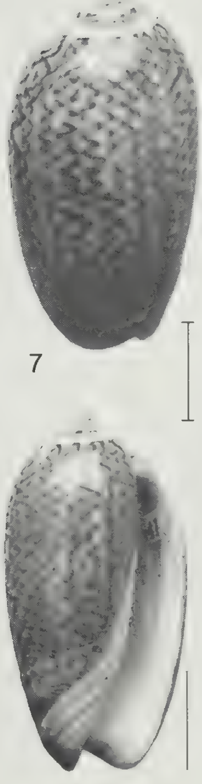
O. foxi
par. AMS


5

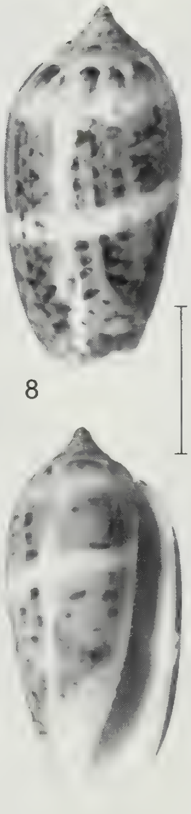
O. spicata
deynzerae


6

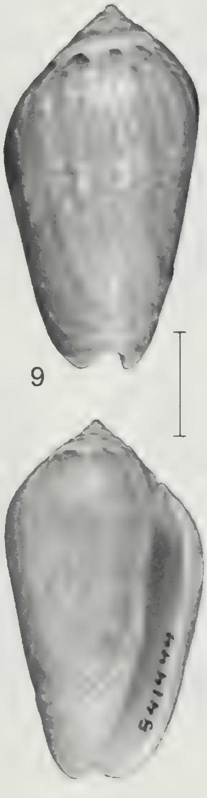
O. polpasta


7

O. truncata


8

O. kerstitchi


9

O. olssoni

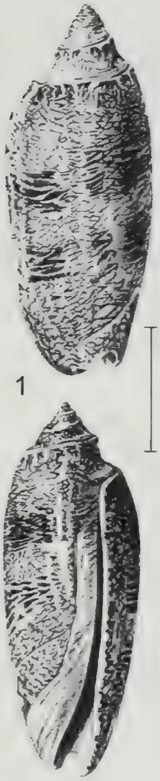
PLATE 5. Type material.

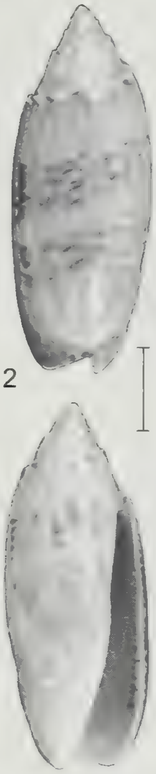
1-4. *O. sayana* Ravenel, 1834.

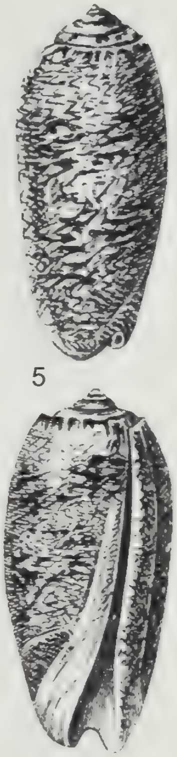
1. *O. litterata* Lamarck (not Röding, 1798), 1811. *Encycl.*, Pl. 362, Figs. 1a, 1b.
2. *O. sayana texana* Petuch & Sargent, 1986. HOLOTYPE USNM 841465 (H: 43.60 mm; D: 17.54 mm). Shallow water, Padre I., off South Texas.
3. *O. sayana sarasotensis* Petuch & Sargent, 1986. HOLOTYPE USNM 841450 (H: 40.60 mm; D: 17.90 mm). 15 m, sand, SCUBA, 15 km West of Lido Beach, Sarasota, Florida.
4. *O. circinata citrina* Johnson, 1911. HOLOTYPE MCZ 6267 (H: 60.51 mm, D: 23.56 mm). "W. Coast Florida".

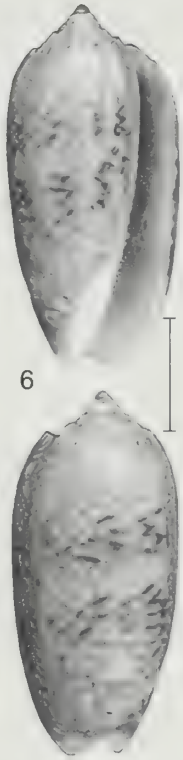
5-10. *O. scripta* Lamarck, 1811.

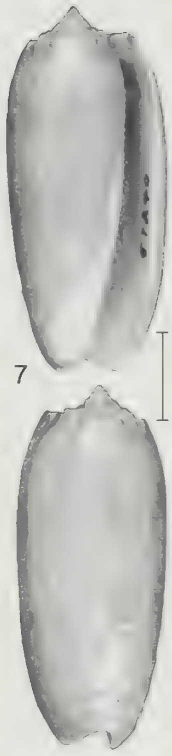
5. *O. scripta* Lamarck (not Röding, 1798), 1811. *Encycl.*, Pl. 362, Figs. 4a, 4b.
6. *O. caribaeensis* Dall & Simpson, 1901. Holotype USNM 159692 (H: 31.61 mm; D: 14.93 mm). Mayaguez, Puerto Rico.
7. *O. trujilloi* Clench, 1938. HOLOTYPE MCZ 57240 (H: 40.52 mm, D: 17.95 mm). "Puerto Plata, Santo Domingo, Dominican Republic. Dredged 30 ft."
8. *O. trujilloi* Clench, 1938. PARATYPE AMNH 79010 (H: 34.8 mm; D: 15.5 mm). "Dredged in 5 fath., Puerto Plata, Santo Domingo".
9. *O. trujilloi* Clench, 1938. PARATYPE (out of five) AMS C.095147, (H: 39.57 mm; D: 18.59 mm). "Suction dredge, 5 m, bluish clay, Puerto Plata, Santo Domingo". Purchased Krause coll., 1972".
10. *O. scripta venezuelana* Petuch & Sargent, 1986. HOLOTYPE USNM 841451 (H: 44.22 mm; D: 22.02 mm). 30 m off Punta Fijo, Paranagua Peninsula, Venezuela.

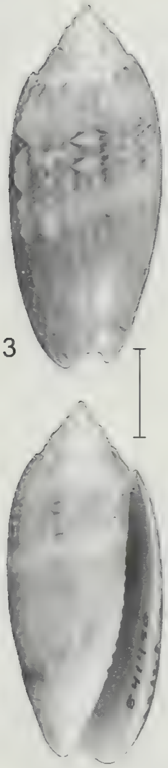
1

O. litterata

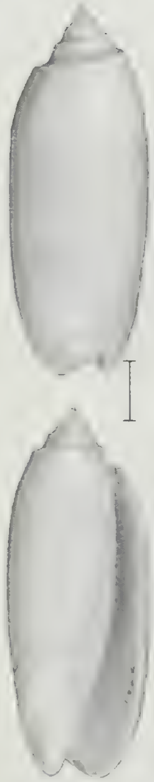
2

O. sayana texana

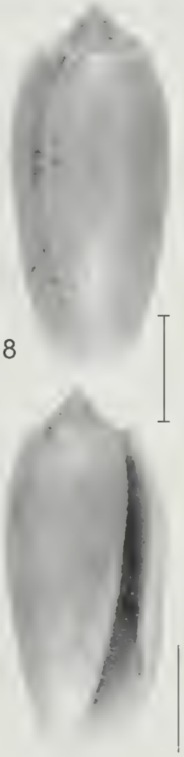
5

O. scripta

6

O. caribaeensis

7

O. trujilloi

3

O. sayana sarasotensis

4

O. sayana citrina

8

O. trujilloi par. AMNH

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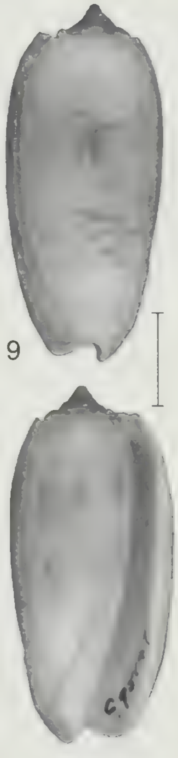
O. trujilloi par. AMS

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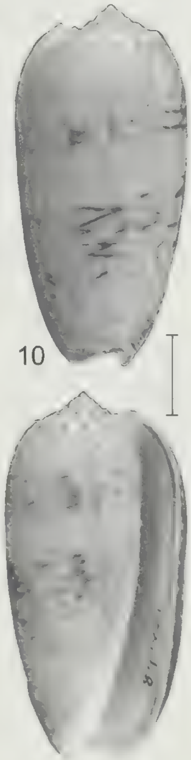
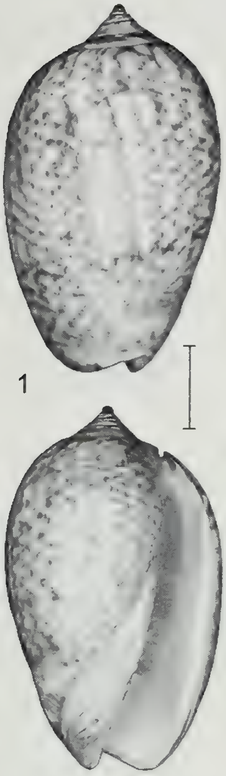

O. scripta venezuelana

PLATE 6. Type material.

1-10. *O. fulgurator* (Röding, 1798).

1. *O. obesina* Duclos, 1840. FIGURED SYNTYPE MNHN (H: 44.0 mm, D: 26.3 mm).
2. *O. aldinia* Duclos, 1845. FIGURED SYNTYPE MNHN (H: 55.6 mm, D: 30.3 mm).
3. *O. porcea* Marrat, 1870. HOLOTYPE MCM (H: 42 mm, D: 20.8 mm).
4. *O. graphica* Marrat, 1870. HOLOTYPE MCM (H: 44.6 mm, D: 22.2 mm).
5. *O. fusiformis* Lamarck, 1811. *Encycl.*, Pl. 367, Figs. 1a, 1b.
6. *O. jamaicensis* Marrat, 1867. HOLOTYPE MCM (H: 37.7 mm, D: 18.4 mm).
7. *O. oblonga* Marrat, 1867. HOLOTYPE MCM (H: 63.2 mm, D: 29.2 mm).
8. *O. magdae* Petuch & Sargent, 1986. HOLOTYPE USNM 841441 (H: 37.57 mm; D: 18.62 mm). In fish trap, 300 m, off Matanzas Bay, Cuba. C. J. Finlay, coll., 1956.
9. *O. mercatoria* Marrat, 1871. SYNTYPE MCM (H: 41.0 mm, D: 19.5 mm).
10. *O. fulgurator* (Röding, 1798). Martini Fig. 562, rotated.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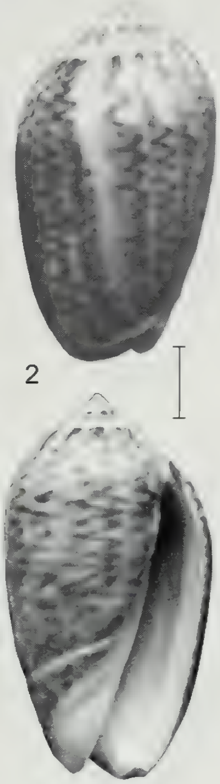
O. obesina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O. aldinia


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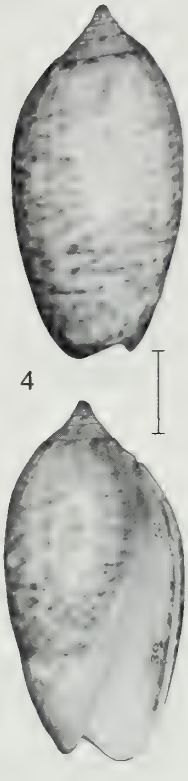
O. porcea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O. graphica


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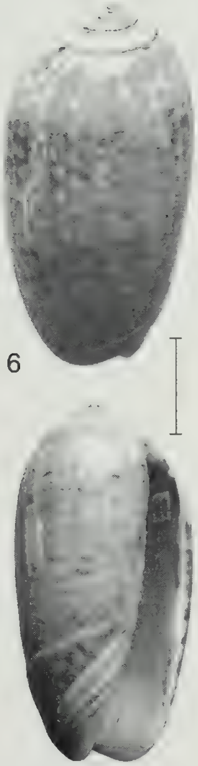
O. fusiformis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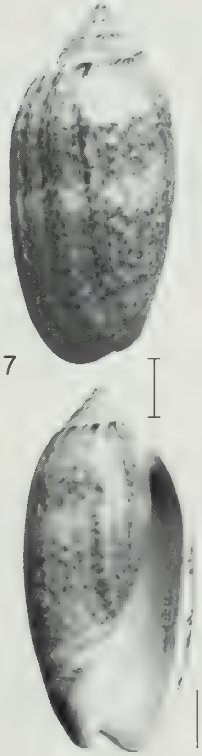
O. jamaicensis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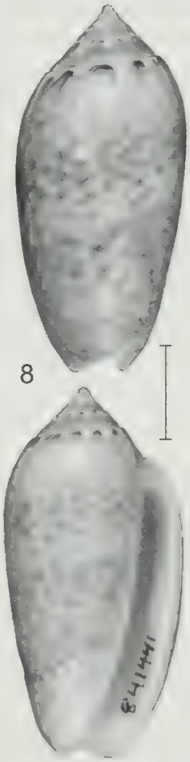
O. oblonga



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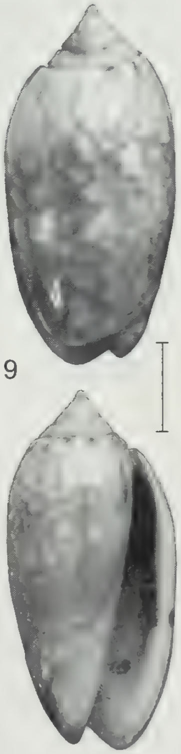
O. magdae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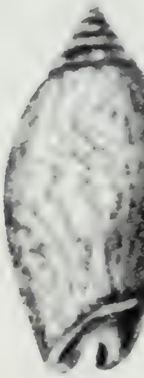
O. mercatoria


10

O. fulgurator

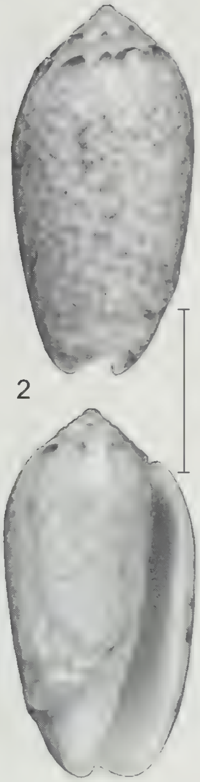
PLATE 7. Type material.

1-9. *O. fulgurator* (Röding, 1798) (continued).

1. *O. timoria* Duclos, 1840. Figured SYNTYPE (out of 3) (H: 62.0 mm; D: 33.1 mm), MNHN.
2. *O. jamaicensis zombia* Petuch & Sargent, 1986. HOLOTYPE USNM 841454. (H: 23.87 mm; D: 12.61 mm). On beach after storm, near sand flats, Southern side of Gonave I. Haiti. 1974.
3. *O. broderipi* Ducros, 1857. HOLOTYPE MNHN (H:27.8 mm; D: 13.4 mm).
4. *O. contoyensis* Petuch, 1988. HOLOTYPE USNM 859945 (H: 36.71 mm; D: 18.42 mm). 35 m. off Contoy I., Yucatan, Mexico.
5. *O. sargenti* Petuch, 1987. Holotype USNM 859864 (H: 28.60 mm; D: 14.03 mm). 5 m, sand, Malmok, Aruba.
6. *O. bifasciata jenseni* Petuch & Sargent, 1986. Holotype USNM 859302 (changed from 841453, Germon *in litt.*.) (H: 50.30 mm; D: 24.12 mm). 0.5 m sand, off Blue Horizons Beach, Bermuda, R. Jensen coll. 1963.
7. *O. drangai* Schwengel, 1951. HOLOTYPE ANSP 247107. (H: 40.47 mm, D: 18.62 mm). Pigeon Pt., Tobago.
8. *O. reticularis bollingi* Clench, 1934. HOLOTYPE MCZ 76656 (H: 61.95 mm, D: 28.52 mm). "Crab-trap, Miami, Florida".
9. *O. nivosa* Marrat, 1871. HOLOTYPE MCM (H: 49.2 mm, D: 22.0 mm).
10. *O. bewleyi* Marrat, 1870. HOLOTYPE MCM (H: 41.8, D: 18.1 mm).


1

O. timoria 2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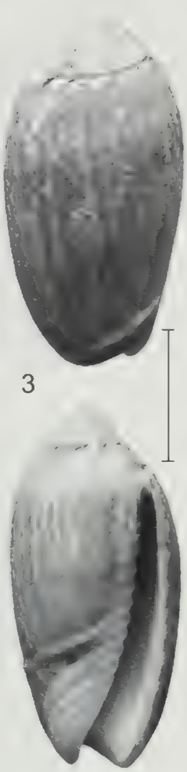
O. jamaicensis zombia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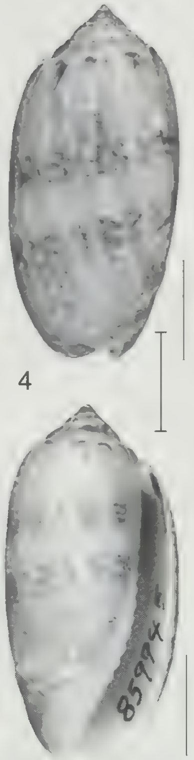
O. broderipi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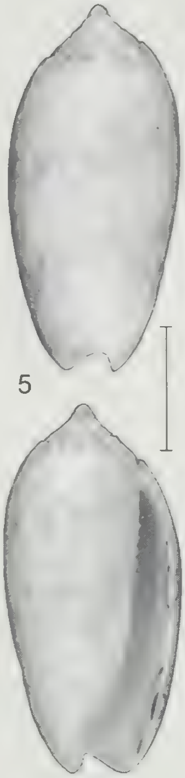
O. contoyensis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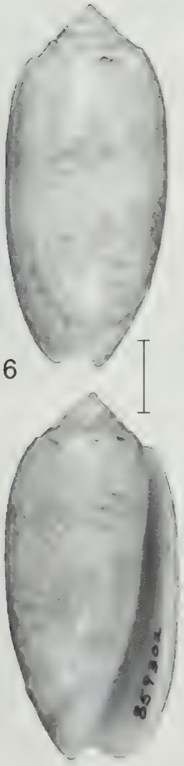
O. sargenti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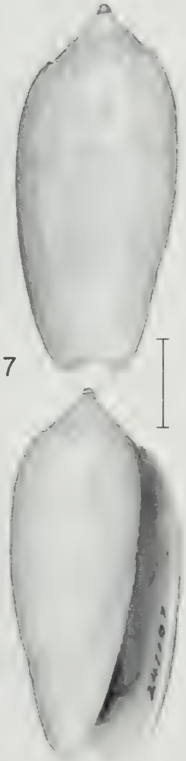
O. bifasciata jenseni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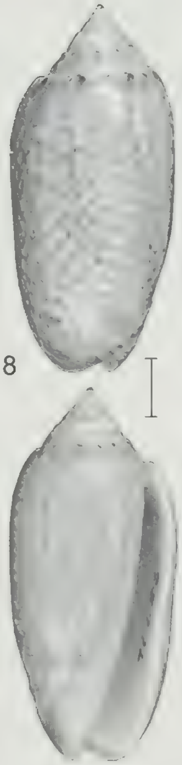
O. drangai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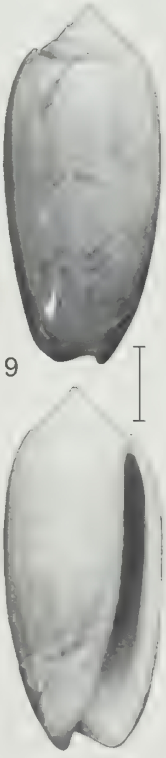
O. reticularis bollingi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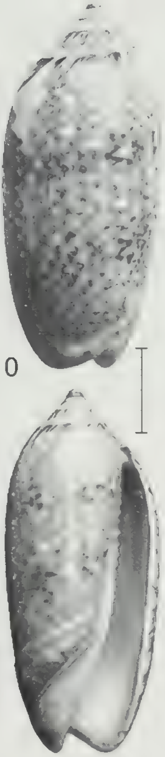
O. nivosa


10

O. bewleyi

PLATE 8. Type material.

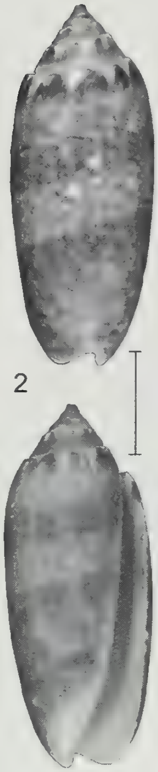
1-10. *O. fulgurator* (Röding, 1798) (continued).

1. *O. maya* Petuch & Sargent, 1986. HOLOTYPE USNM 859301 (changed from 841453, Germon *in litt.*) (H: 57.81 mm: D: 24.97 mm). Trawled by shrimper in 35 m. off Contoy Is., Yucatan, Mexico. 1977.
2. *O. goajira* Petuch & Sargent, 1986. HOLOTYPE USNM 841433 (H: 36.79 mm; D: 15.49 mm). 60 m off Cabo La Vela, Colombia.
3. *O. figura* Marrat, 1870. Holotype MCM (H: 41.2 mm, D: 18.1 mm).
4. *O. bifasciata* Küster in Weinkauff, 1878. FIGURED SPECIMEN SMF 9353. (H: 61.39 mm, D: 26.73 mm). "Brasilien".
5. *O. reticularis greenwayae* Clench, 1937. HOLOTYPE MCZ 115455 (H: 59.65 mm, D: 25.18 mm). "Smith Point, Grand Bahama Island, Bahamas".
6. *O. reticularis pattersoni* Clench, 1945. HOLOTYPE MCZ 151166 (H: 62.57 mm, D: 28.29 mm). "5 miles E of Crabbing Point, Great Bahama Island, Bahamas".
7. *O. ernesti* Petuch 1990. Holotype USNM 860535. (H: 33.66 mm, D: 15.45 mm) (not H: 38 mm as in description). Trawled 40m silty sand, off Portobello, Panama (East).
8. *O. finlayi* Petuch & Sargent, 1986. HOLOTYPE USNM 841432 (H: 39.98 mm; D: 18.71 mm). 200 m, Matanzas Bay, Cuba.
9. *O. reticularis* Lamarck, 1811. *Encycl.*, Pl. 361, Figs. 1a, 1b.
10. *O. bahamasensis* Petuch & Sargent, 1986. Holotype USNM 841426 (H: 44.58 mm; D: 20.62 mm). In lobster pot, in 200 m off Grand Bahama I., Bahamas.

1

O. maya

2



O. goajira

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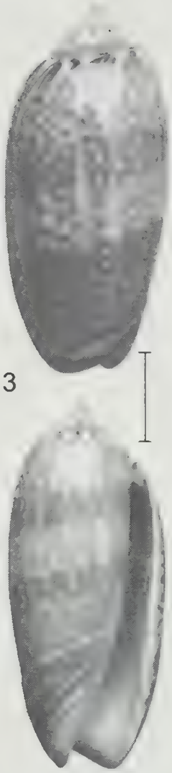

O. figura

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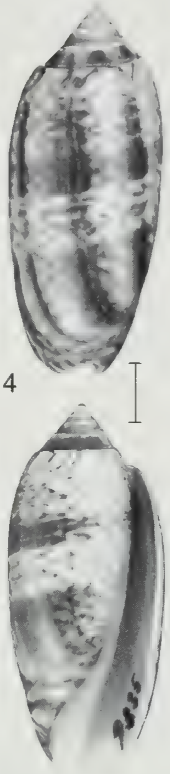
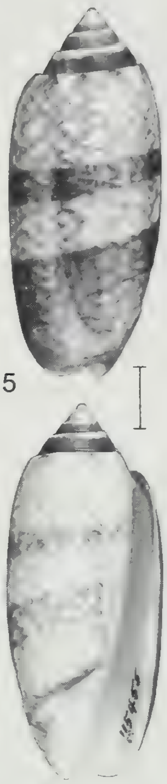


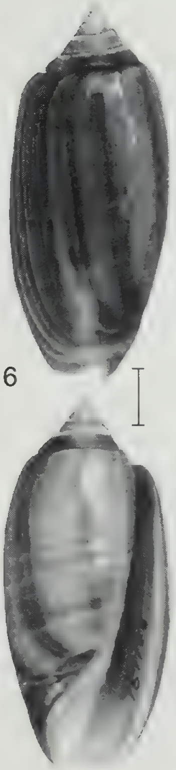
O. bifasciata

5



O. reticularis greenwayae

6



O. pattersoni

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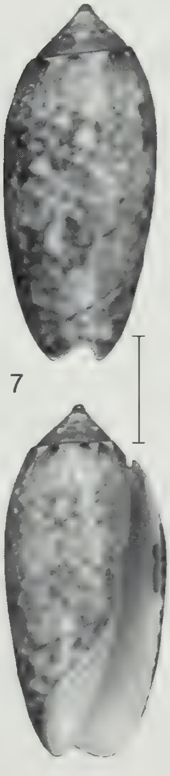

O. ernesti

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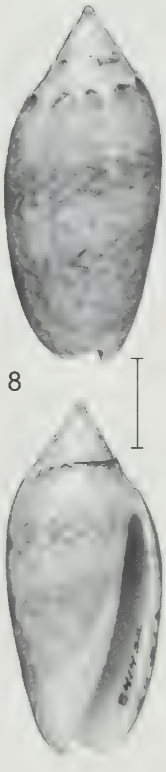

O. finlayi

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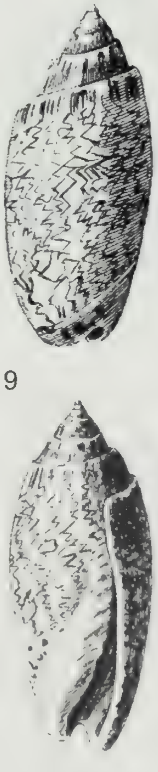

O. reticularis

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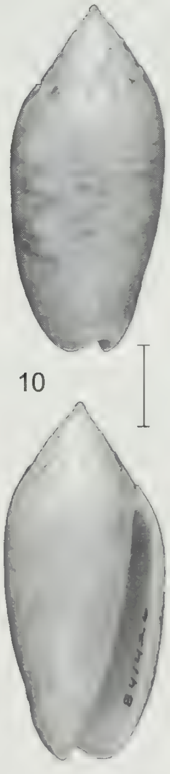


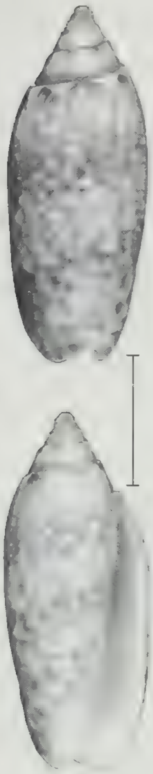
O. bahamensis

PLATE 9. Type material.

1-10. *O. fulgurator* (Röding, 1798) (continued).

1. *O. antillensis* Petuch & Sargent, 1986. Holotype USNM n° 841425 (H: 28.05 mm; D: 11.47 mm). On sand flats, low tide, at night, Southern coast of Gonave Island, Haiti.
2. *O. olorinella* Duclos, 1835. Syntype MNHN (H: 28.7 mm; D: 12.1 mm.).
3. *O. bullata* Marrat, 1871. Holotype MCM (H: 60.83 mm; D: 26.21 mm).
4. *O. barbadensis* Petuch & Sargent, 1986. Holotype USNM 841427 (H: 47.05 mm; H: 20.32 mm). 200 m off St. James, Barbados.
5. *O. bifasciata sunderlandi* Petuch, 1987. Holotype USNM 859904 (H: 22.02 mm; D: 9.56 mm). Trawled 150 m West of Cedar Key, Florida.
6. *O. formosa* Marrat, 1870. Holotype MCM (H: 45.23 mm; D: 19.52 mm).
7. *O. reclusa* Marrat, 1871. Holotype MCM (H: 43.2 mm, D: 18.1 mm).
8. *O. circinata* Marrat, 1871. Holotype MCM (H: 55.4, D: 23.4 mm).
9. *O. circinata tostesi* Petuch, 1987. Holotype USNM 859865 (H: 46.20 mm; D: 21.37 mm) (not H: 41 mm as in description). 1 m, sand, Ilha Cabra, Illhabela, Sao Paulo State, Brazil.
10. *O. cribraria* Marrat, 1883? Holotype MCM (H: 48.22 mm; D: 22.12 mm).

1



O. antillensis

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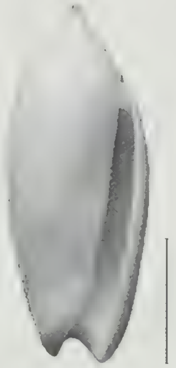

O. olorinella

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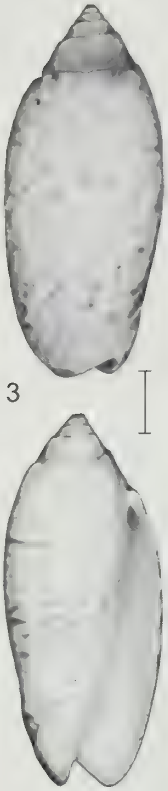

O. bullata

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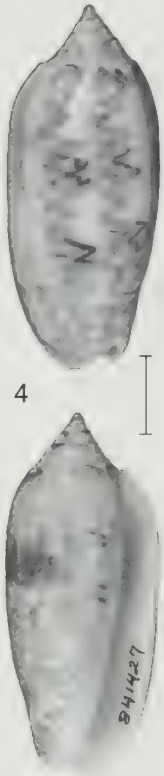

O. barbadensis

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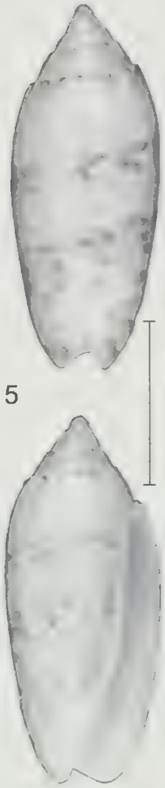

O. bifasciata sunderlandi

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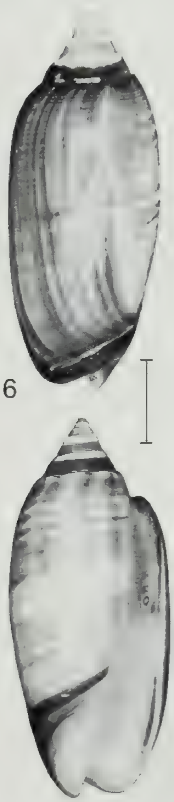

O. formosa

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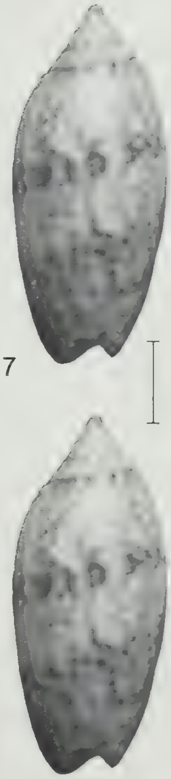

O. reclusa

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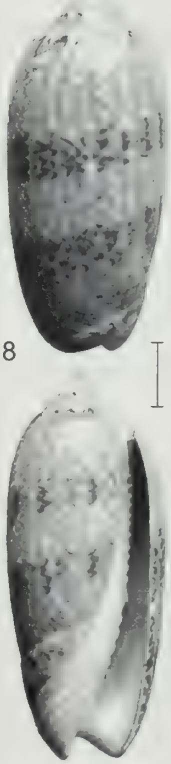

O. circinata

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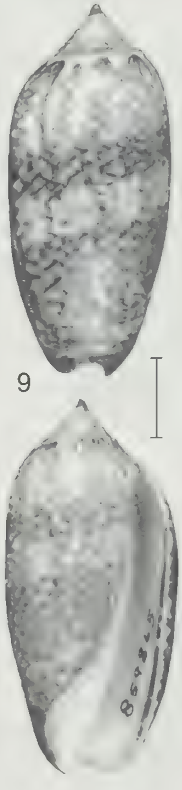

O. circinata tostesi

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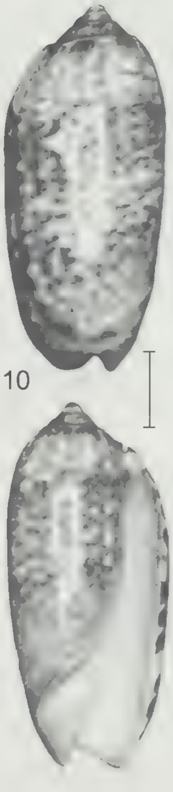
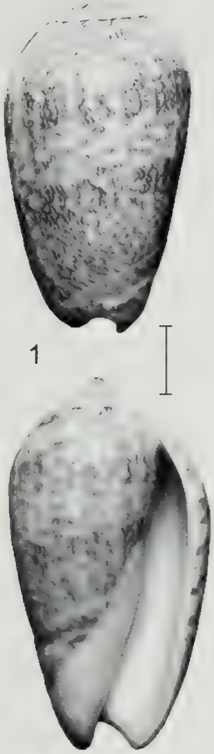


O. cribraria

PLATE 10. Type material.

1-10. *O. spicata* (Röding, 1798).

1. *O. timoria* Duclos, 1840. Figured SYNTYPE (out of 3) (H: 55.8 mm; D: 39.1 mm), MNHN.
2. *O. pindarina* Duclos, 1840. FIGURED SYNTYPE MNHN (H: 53.4mm; D: 27.3 mm).
3. *O. ligneola* Reeve, 1850. SYNTYPE (out of 2) BM(NH) 1892.9.24.4-5 (H: 25.60 mm; D: 13.09 mm). "Loc? Purchased of Miss Steere".
4. *O. punctata* Marrat, 1870: SYNTYPE (out of two) MCM (H: 35.35 mm; D: 17.24 mm).
5. *O. spicata* (Röding, 1798). Martini's figures 509 and 510 (rotated, cast shadow removed for better legibility).
6. *O. radix* Petuch & Sargent, 1986. HOLOTYPE USNM 841446 (H: 36.62mm; D: 22.51 mm).. 75m, off Isla la Plata, Ecuador.
7. *O. subangulata corteziana* Petuch & Sargent, 1986. HOLOTYPE USNM 841457 (H: 32.33 mm; D: 16.21 mm). Northern end of the Gulf of California.
8. *O. spicata hemphilli* Johnson, 1911. SYNTYPE (out of five) ANSP 111697 (H: 54.05 mm, D: 23.38 mm). "San Ignacio Lagoon, Lower California. John Ford colln."
9. *O. rejecta* Burch & Burch, 1962. PARATYPE MNHN (H: 31.3, D: 13.6 mm). La Paz, Baja California, Mexico.
10. *O. rejecta* Burch & Burch, 1962. PARATYPE USNM 667317 (H: 37.24 mm; D: 16.01 mm). La Paz, Baja California, Mexico.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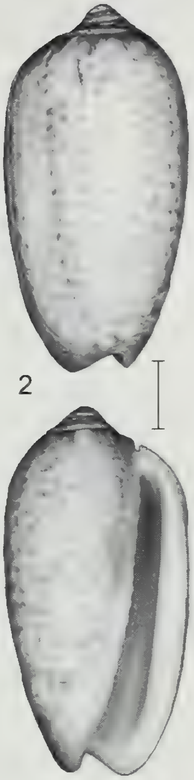
O. timoria 1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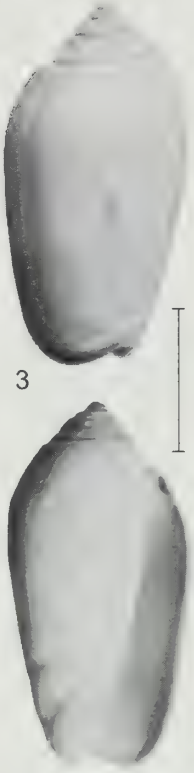
O. pindarina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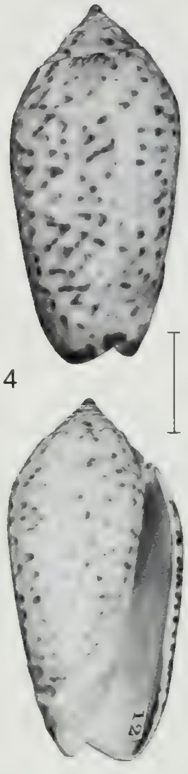
O. ligneola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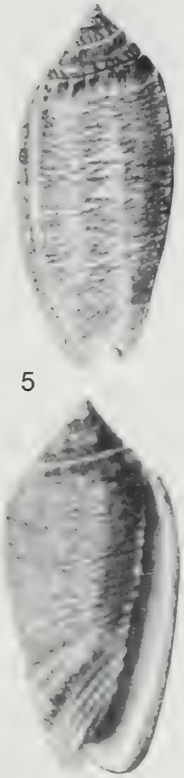
O. punctata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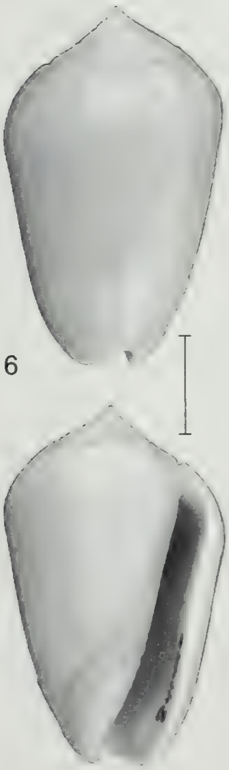
O. spicata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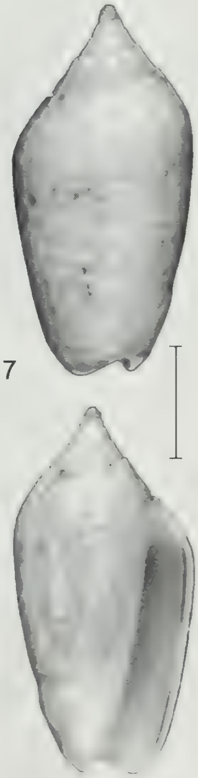
O. radix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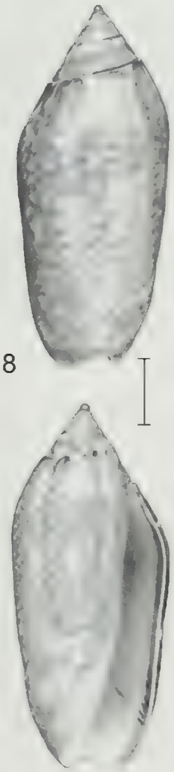
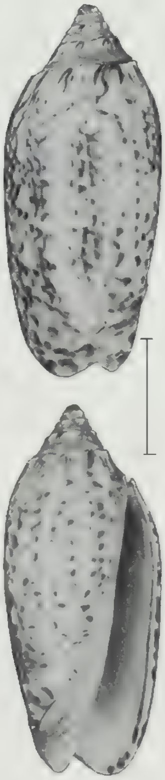
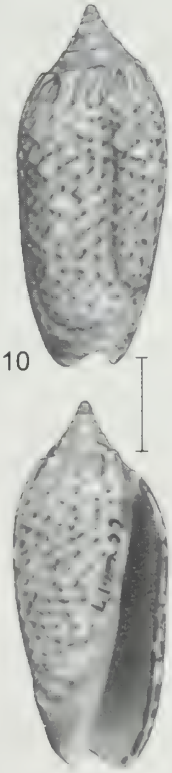
O. subangulata corteziana


8

O. spicata var. hemphilli


9

O. rejecta par. MNHN


10

O. rejecta par. USNM

PLATE 11. Type material.

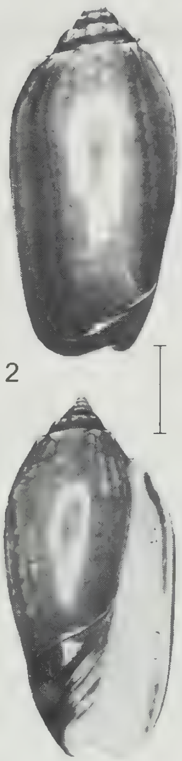
1-8. *O. spicata* (Röding, 1798) (continued).

1. *O. cumingii* Reeve, 1850. SYNTYPE (out of 3) BM(NH) 1987008 (H: 48.4 mm; D: 24.2 mm). "Gulf of California. H. Cuming colln."
2. *O. fuscata* Marrat, 1870. SYNTYPE (out of 3) MCM (H: 42.66 mm; D: 20.30 mm).
3. *O. brunnea* Marrat, 1870. HOLOTYPE MCM (H: 34,0 mm, D: 16.1 mm).
4. *O. oniska* Duclos, 1844. FIGURED SYNTYPE MNHN (H: 61.0 mm; D: 26.2 mm).
5. *O. spicata perfecta* Johnson, 1911. SYNTYPE (out of three) ANSP 111729 (H: 59.06 mm, D: 25.73 mm). "West Coast Central America. John Ford colln."
6. *O. subangulata* Philippi, 1848. SYNTYPE (out of two) BM(NH) 1924.1.5.98-99. (H: 59.62 mm; D: 26.38 mm).
7. *O. fuscata* Marrat, 1870. Another SYNTYPE (out of 3) MCM (H: 39.76 mm; D: 18.62 mm).
8. *O. violacea* Marrat, 1867.
9. *O. intertincta* Carpenter, 1857. SYNTYPE (largest of two) USNM 716187, (both specimens numbered with ink "592/2121") (H: 19.68 mm; D: 9.70 mm). Mazatlan, Sinaloa, Mexico, ex coll. F. REIGEN.
10. *O. ionopsis* Berry, 1969. Holotype SMBNH 34656 (H: 30.54 mm; D: 13.76 mm). 33fms, Bahia de las Palmas, Baja California.

1

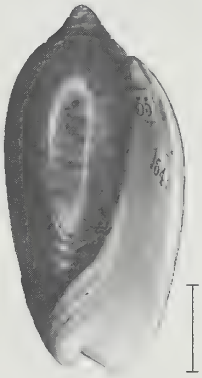
O. cumingi

2



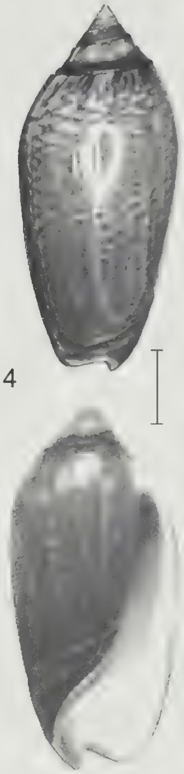
O. fuscata 1

3



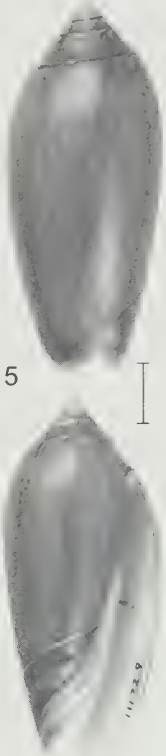
O. brunnea

4



O. oniska

5

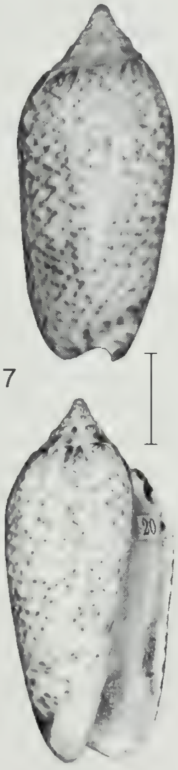


O. spicata var. perfecta

6

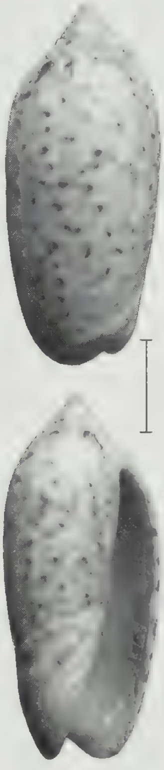
O. subangulata

7



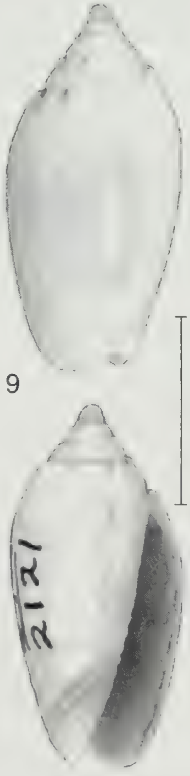
O. fuscata 2

8



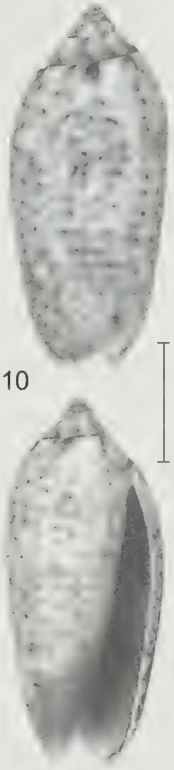
O. violacea

9



O. intertincta

10



O. ionopsis

Un nouveau genre de Pholadidae (Mollusca, Bivalvia) du Paléogène inférieur du nord de l'Atlantique

Jean-Michel PACAUD

5, Avenue Pablo Picasso - F - 94120 Fontenay-sous-Bois, France

MOTS CLES. Pholadidae, Paléogène inférieur, Atlantique, Europe, Etats Unis, Systématique.

KEYWORDS. Pholadidae, Early Paleogene, Atlantic Ocean, Europe, United States, Systematics.

RESUME. La position systématique de toutes les espèces de la sous-famille des Pholadinae du Paléogène inférieur est revue. Les caractères morphologiques propres à ces espèces permettent de les séparer du genre *Barnea* où elles étaient jusqu'ici classées. La comparaison avec les autres genres de Pholadinae conduit à proposer un nouveau genre, *Cyrtopleuropsis.* Ces espèces sont seulement connues en Atlantique et sont les suivantes: pour l'Europe, *Cyrtopleuropsis orbignyana* (Lévesque *in* Graves, 1847); *C. freyteti* (Plaziat, 1970); *C. lescailloni* nov. sp. et pour les Etats-Unis, *C. alatoidea* (Aldrich, 1886). Une distribution stratigraphique de l'ensemble des Pholadinae cénozoïques est donnée.

ABSTRACT. The aim of this work is a review of the systematics of all Pholadinae from the Lower Paleogene. Except *Cyrtopleuropsis lescailloni* wich is new, these species are currently assigned in the genus *Barnea.* However comparisons with *Barnea* and other genera of Pholadinae show distinctive morphological characters wich permit to propose a new genus, *Cyrtopleuropsis.* Paleogene species are only know an Atlantic Ocean: for the Europe,*Cyrtopleuropsis orbignyana* (Lévesque *in* Graves, 1847); *C. freyteti* (Plaziat, 1970); *C. lescailloni* nov. sp. and for the United States, *C. alatoidea* (Aldrich, 1886). Stratigraphic distribution is given for all caenozoic Pholadinae.

INTRODUCTION

L'Examen des Pholadinae du Paléogène inférieur du Nord de l'Atlantique m'avais conduit à rapporter *Pholas orbignyana* (Lévesque *in* Graves, 1847), de l'Eocène du Bassin Anglo-parisien, dans le genre *Cyrtopleura* Tryon, 1862 (LE RENARD & PACAUD, 1995). De nouvelles récoltes de ce matériel rare et généralement mal conservé permettent des observations supplémentaires pour préciser la position systématique de ce groupe de Pholadidae, aboutissant à proposer un nouveau genre: *Cyrtopleuropsis.*

Abbréviations utilisées

MNHN-LP: Laboratoire de Paléontologie. Muséum National d'Histoire Naturelle de Paris.

MNHN-BIMM: Laboratoire de Biologie des Invertébrés Marins et Malacologie. Muséum National d'Histoire Naturelle de Paris.

UPMC: Service de la collection de Paléontologie, Université Pierre et Marie Curie, Paris VI.

BMNH: The Natural History Museum, Londres.

USNM: National Museum of Washington.

PRI: Paleontological Research Institution, Ithaca, New York.

ETUDE SYSTEMATIQUE

Famille: **PHOLADIDAE** Lamarck, 1809

Sous-Famille: **Pholadinae** Lamarck, 1809

Genre: ***Cyrtopleuropsis*** nov. gen.

Espèce-type: *Pholas orbignyana* Lévesque *in* Graves, 1847 (= *Pholas levesquei* Watelet, 1851)

Derivatio nominis. Forme fossile rappelant par sa morphologie le genre *Cyrtopleura.* Genre grammatical: féminin.

Diagnose. Coquille allongée. Bord antérieur acuminé. Bord postérieur atténué. Bord antéro-ventral échancré et sinueux. Bord cardinal retourné sur le crochet. Réflexion umbonale non cloisonnée. Charnière pourvue d'un chondrophore. Apophyse large et arrondie. Surface dorsale présentant une sculpture radiaire s'interrompant à mi-longueur de la valve, découpant en festons le bord antérieur. Région dorso-postérieure marquée par de nombreuses granulations.

Distribution. La présence de Pholades dans le Bassin de Paris fut relevée pour la première fois dans le Cuisien par Lévesque (1847) avec *Pholas orbignyana.* L'espèce fut découverte plus tard par l'abbé LAMBERT dans les sables sparnaciens de Sinceny (Aisne). D'après un moule interne provenant de la collection Armand BAZIN, DESHAYES (1857, p. 135) signale *P. orbignyana* du Thanétien de Gannes (Oise). PERREAU (WYNS & *al.*, 1981, p. 50) cite avec doute cette espèce du Thanétien de Bachivillers (Oise) d'après une valve incomplète (matériel non conservé, comm. Perreau). DESHAYES (1857, p. 135) signale aussi *P. orbignyana* au Lutétien d'après des fragments provenant de Grignon (Yvelines) et un exemplaire récolté par DUTEMPLE à Damery (Marne). L'espèce est également signalée par de nombreux auteurs dans l'Eocène d'Angleterre. Au Paléocène des Etats-Unis, une autre espèce est décrite par ALDRICH (1886) de Gregg's Landing (Alabama), *Pholas alatoidea.* PLAZIAT (1970) a décrit une espèce du Sparnacien des Corbières septentrionales, *Barnea freyteti*, proche de *Pholas orbignyana.*

Discussion générique. La fragilité du test des Pholades rend très rare la conservation complète à l'état fossile de leurs valves et de leurs plaques accessoires (protoplax, mesoplax et metaplax). Après la mort de l'animal, ces plaques accessoires sont dispersées et généralement détruites. Leurs formes énigmatiques furent à l'origine de méprises de la part de divers auteurs. COSSMANN (1907, p. 201-202) décrit l'apophyse de *Cyrtopleuropsis orbignyana* comme *Avicula moloti* du Sparnacien de Pourcy (Marne). Des protoplax ou des apophyses furent aussi déterminés comme *Scutum, Crepidula, Acmaea* ou *Patella* (TURNER, 1954). Ces plaques accessoires permettent une distinction générique. Les protoplax de *Barnea* Leach *in* Risso, 1826 à sillon médian prononcé et de *Anchomasa* Leach, 1852 sans sillon médian se distinguent de celui de *Monothyra* Tryon, 1862 plus triangulaire et de celui de *Cyrtopleura* Tryon, 1862, en forme de T. LAURIAT-RAGE & MAKINSKY (1983) ont signalé la présence de plusieurs protoplax d'une pholade dans le Miocène moyen de Thenay (Indre-et-Loire) et ont ainsi pu rapporter au sous-genre *Monothyra*, l'espèce *Pholas dujardini* Mayer, 1859. GLIBERT & VAN DE POEL (1966, p. 14-15) plaçaient alors cette dernière dans le sous-genre *Thovana* Gray, 1947.

Aucune de ces plaques n'a été retrouvée dans le Bassin de Paris. De ce fait l'interprétation générique fondée sur le protoplax ne peut être établie et repose donc sur la forme de la coquille, de l'apophyse et sur la présence à la charnière d'un chondrophore, modification de la charnière servant de surface d'insertion au résilium.

Les genres *Pholas (s. str.)* Linné, 1758 (espèce-type *P. (s. str.) dactylus* Linné, 1758), *Pholas (Thovana)* Gray, 1847 (espèce-type *P. (Thovana) campechiensis* Gmelin, 1791), et *Pholas (Monothyra)* Tryon, 1862 (espèce-type *P. (Monothyra) orientalis* Gmelin, 1791) (Figs. 23-28) se caractérisent par le cloisonnement alvéolaire de la réflexion umbonale et diffèrent donc des coquilles paléogènes. Chez l'espèce-type de *Barnea (s. str.)* Leach *in* Risso, 1826, *B. (s. str.) candida* (Linné, 1758), l'ornementation radiaire atteint l'extrémité postérieure, l'échancrure antéro-ventrale est à peine indiquée et l'extrémité antérieure est arrondie, non baillante, l'apophyse est d'une forme étroite et courbe. Un chondrophore est présent chez *B. candida*, cependant il est nettement plus faible et moins projeté que celui des coquilles paléogènes (Figs. 29-30). L'échancrure antéro-ventrale des coquilles paléogènes rappelle celle de *Zirfaea* Leach *in* Gray, 1847 (espèce-type *Zirfaea crispata* (Linné, 1758) (Figs. 33-34), mais la région médiane des valves de *Zirfaea* montre un sulcus umbono-ventral,correspondant à la clavicule de la face interne, ce qui exclut tout rapprochement. L'espèce-type du sous-genre *Barnea (Anchomasa)* Leach, 1852, *B. (Anchomasa) parva* (Pennant, 1777) est plus proche par son échancrure antéro-ventrale sinueuse, par son extrémité antérieure en forme de rostre ainsi que par ses côtes radiaires s'interrompant à mi-longueur de la valve (Figs. 31-32). Toutefois la forme des valves, tordue, courte et large, souvent tronquée dans la région postérieure, l'échancrure ventrale plus longue (elle atteint la moitié de la longueur totale), la forme de son apophyse, étroite et fortement courbée, écartent tout autre rapprochement avec les coquilles paléogènes.

C'est finalement avec les coquilles de *Cyrtopleura (s. str.)* Tryon, 1862 et *Cyrtopleura (Scobinopholas)* Grant & Gale, 1931 que *Cyrtopleuropsis* s'apparente le plus (tableau 1). L'ornementation des coquilles paléogènes concorde assez bien avec celle de l'espèce-type de *Cyrtopleura (s. str.), C. (s. str.) cruciger* (Sowerby, 1834). Toutefois les valves de cette dernière présentent une sculpture radiaire se poursuivant au-delà de la région médiane, s'atténuant progressivement au lieu de cesser brusquement vers le milieu de la longueur (Figs. 19-20). L'apophyse est d'une forme étroite, fortement courbée et creusée, alors que celles observées encore en place sur les charnières de *Cyrtopleuropsis orbignyana* (Lévesque *in* Graves, 1847), de *C. alatoidea* (Aldrich, 1886) et de *C. lescailloni* sont plus petites, plus larges et plus arrondies. Les fortes côtes radiaires de la région antérieure de *Cyrtopleuropsis* rappellent celles que l'on observe chez l'espèce-type du sous-genre *Scobinopholas* Grant & Gale, 1931, *Cyrtopleura (Scobinopholas) costata* (Linné, 1758); toutefois chez *Scobinopholas* la sculpture radiaire persiste sur toute la surface dorsale des valves et le bord antérieur est nettement arrondi (Figs. 21-22), l'apophyse est large et arrondie. Les empreintes musculaires nettes ainsi que le sinus palléal large et profond de *Cyrtopleura (s. str.)* rappelle assez celui de

Cyrtopleuropsis. Chez *Scobinopholas* le sinus palléal est invisible et certaines coquilles de *Cyrtopleura (Scobinopholas) costata* montrent, en dessous de l'empreinte de l'adducteur postérieur, une saillie donnant plus d'assise pour l'attache du muscle. La présence chez *Cyrtopleuropsis* d'un chondrophore, visible seulement chez quelques Pholades, notamment chez *Cyrtopleura (s. str.)*, la rapproche du groupe *Cyrtopleura-Scobinopholas*. Il faut cependant remarquer l'absence de granulations sur la surface dorso-postérieure et d'échancrure ventrale chez *Cyrtopleura* et *Scobinopholas*. L'extrémité antérieure, arrondie et à peine baillante, contraste avec les coquilles paléogènes. TRACEY (communication personnelle) observe que *C. orbignyana* ne se récolte que dans des gisements à substrat non induré. *C. orbignyana* se rencontre dans des gisements tels que Abbecourt, Bachivillers, Cuise-la-Motte, Pierrefonds, Trosly-Breuil, Liancourt-Saint-Pierre, Le Rocquet et Sinceny où le substrat semble avoir été sableux ou sablo-vaseux. Ceci va dans le sens de notre rapprochement générique car les *Cyrtopleura* actuelles sont inféodées aux substrats meubles, tandis que *Barnea*, genre dans lequel les auteurs classaient jusqu'ici les diverses espèces discutées ici, creuse des niches dans la roche. Une morphologie et une écologie comparable suggèrent des relations étroites entre *Cyrtopleuropsis* et les genres *Cyrtopleura* et *Scobinopholas* qui en dérivent probablement (d'où le rapprochement fait par TRACEY (1986), LE RENARD & PACAUD (1995) et JEFFERY & TRACEY (1997) pour *Pholas orbignyana*).

	Cyrtopleuropsis	*Cyrtopleura*	*Scobinopholas*	*Pholas*	*Monothyra*	*Thovana*	*Barnea*	*Anchomas*	*Zirfaea*
Présence de granulations sur la face dorsale	•	-	-	-	-	-	-	-	
Plaques accessoires	inconnues	•	•	•	•	•	•	•	•
Présence d'un chondrophore	•	•	•	-	-	-	•	-	-
Réflexion umbonale simple	•	•	•	-	-	-	•	•	•
Réflexion umbonale cloisonnée	-	-	-	•	•	•	-	-	-
Apophyse large (Fig. 7)	•	-	•	-	•	-	-	-	-
Apophyse étroite (Fig. 30)	-	•	-	•	-	•	•	•	•
Sinus palléal large et profond	•	•	invisible	•	invisible	•	invisible	•	•
Empreintes musculaires bien marquées	•	•	•	•	faibles	•	faibles	faibles	•
Présence d'une échancrure antéro-ventrale	•	-	-	•	-	-	-	•	•
Présence d'un sulcus umbono-ventral	-	-	-	-	-	-	-	-	•
Ornementation radiaire s'interrompant à mi-longueur de la valve	•	-	-	-	-	-	-	•	•
Ornementation radiaire couvrant la totalité de la surface dorsale	-	-	•	-	-	-	•	-	-
Ornementation radiaire s'attenuant au-delà de la mi-longueur de la valve	-	•	-	•	•	•	-	-	-

Tableau 1.

Cyrtopleuropsis orbignyana
(Lévesque in Graves, 1847) nov. comb.
(Figs, 1-9 et 13)

1847 *Pholas Orbignyana* Lévesque *in* Graves : 643.

Synonymie:
1851 *Pholas Levesquei* Watelet : 11, pl. I, fig. 1-5.
1906 *Avicula? Moloti* Cossmann & Pissarro : pl. XLV, fig. 121-14.
1907 *Avicula Moloti* Cossmann & Pissarro : 201-202, pl. VII, fig. 121-14.
1963 *Barnea cf. levesquei* (Watelet) - Stinton : 68-69, pl. 8, fig. 1-5; pl. 9, fig. 1-2.
1963 *Barnea cingulata* Stinton : 69, pl. 8, fig. 6a-b.
1981 *Barnea* sp. Perreau *in* Wyns & *al.* : 50.

Autres références:
1850 *Pholas orbignyana* Lévesque *in* Graves - d'Orbigny : 321, n° 439.
1856 *Pholas Levesquei* Watelet - Deshayes : pl. VI, fig. 10-12; p. 135-136 (1857).
1882 *Pholas Levesquei* Watelet - Zittel : 138, fig. 197a-b.
1885 *Pholas Orbignyi* Lévesque *in* Graves - Chelot : 192.
1886 *Pholas Levesquei* Watelet - Fritel : pl. II, fig. 9.
1886 *Barnea Levesquei* (Watelet) - Cossmann : 13.
1891 *Dactylina Levesquei* (Watelet) - Newton : 94.
1930 *Barnea levesquei* (Watelet) - Wrigley : 378.
1986 *Cyrtopleura levesquei* (Watelet) - Tracey : 118.
1995 *Cyrtopleura orbignyana* (Lévesque *in* Graves) - Le Renard & Pacaud : 67.

1996 *Cyrtopleura orbignyana* (Lévesque *in* Graves) - Pacaud & Le Renard : 184.
1996 *Cyrtopleura levesquei* (Watelet) - Tracey, Todd, Le Renard, King & Goodchild : 136-137.
1997 *Cyrtopleura levesquei* (Watelet) - Jeffery & Tracey : 89-90, pl. 6, fig. 15.

Localité-type. Cuise-la-Motte (Oise), Cuisien.

Distribution de l'espèce. Thanétien - Yprésien (Paléocène - Eocène).

Matériel-type. Non retrouvé.

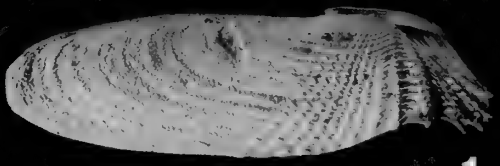
Matériel thanétien. Sables de Bracheux, Bachivillers, lieu-dit " Remise Madame " (Oise): 1 valve gauche, Fig. 5 (coll. Pons); 1 fragment, valve droite (coll. Pacaud, lot n° P25359); 1 fragment, valve droite (coll. Lescaillon); Abbecourt, lieu-dit " Bois des Godins " (Oise): 1 fragment (coll. Pacaud, lot n° P24889).

Autre matériel examiné. Cuisien: Cuise-la-Motte (Oise), 1 valve droite, longueur: 32 mm., Figs. 1-2 (coll. Lhomme, MNHN-LP, lot n° B50646), 1 valve gauche, longueur: 27 mm., Figs. 3-4 (coll. Lhomme, MNHN-LP, lot n° B50646); 1 valve droite mutilée, Figs. 6-7 (coll. Pacaud, lot n° P32275), 1 valve gauche incomplète, Figs. 8-9 (coll. Pacaud, lot n° P32275); 20 valves (coll. Marceaux, MNHN-LP); Pierrefonds (Oise): 23 exemplaires en connection (coll. Munier-Chalmas, UPMC); Trosly-Breuil (Oise): 1 valve droite (coll. Pacaud, lot n° P36113); Le Roquet (Oise): 2 valves gauches et 1 valve droite incomplètes (coll. Pacaud, lot n° P36304). Sparnacien: Sinceny (Aisne): 2 valves droites incomplètes (coll. Pacaud, lot n° P45360).

Description du matériel thanétien. Coquille de 97 mm. de long et de 29 mm. de large, fortement inéquilatérale. Bord antérieur acuminé, terminé par un rostre. Bord postérieur long et atténué. Bord antéro-ventral échancré et sinueux. Bord cardinal fortement retourné, enveloppant le crochet. Réflection umbonale sinueuse et non cloisonnée. Chondrophore bilobé, lame inférieure courte. Apophyse large et arrondie. Surface dorsale présentant toujours, dans la région antérieure, une sculpture radiaire composée de 16 côtes fortement marquées dans le test s'interrompant à mi-longueur de la valve. Les huit premières sont puissantes, largement espacées, gravant profondément leurs empreintes dans la face interne de la valve; se comportant comme des carènes lisses sur la face interne de la valve, se projetant en pointes aiguës sur le bord antéro-ventral, le découpant en festons plus ou moins profonds. Sur la face externe, les côtes sont en revanche puissamment sculptées de chevrons épineux imbriqués les uns dans les autres. La sculpture radiaire qui suit est constituée de 8 autres côtes plus rapprochées et cesse brusquement vers le milieu de la longueur. Leur ornementation est plus faible. La surface interne des valves conserve également leurs traces sous la forme de lignes martelées par les petites écailles externes. Elles sont bien moins gravées dans le test que les huit premières et leur inclinaison umbono-antéro-ventrale est à l'opposé de ces dernières. La région postérieure est parcourue de lignes de croissance sublamelleuses, régulières, faiblement marquées et de très nombreuses granulations rappelant celles qui peuvent s'observer à la surface de *Panopea* Ménard ou de *Poromya* Forbes. L'impression du muscle adducteur postérieur est ovale, étroite et allongée. Le sinus palléal est large, aigu en sa partie palléo-ventrale, remontant très haut vers l'impression, petite et ovalaire, du muscle adducteur antérieur.

Comparaison avec le matériel cuisien. La sculpture de la face dorsale et l'inclinaison umbono-antéro-ventrale des costules rayonnantes sont identiques lorsque l'on compare la valve de la Figure 5 du Thanétien et celles des des Figures 1- 4 du Cuisien de Cuise-la-Motte. D'autre part, l'identité des valves du Cuisien et de celles du Thanétien se retrouve sur les traces musculaires, le chondrophore et l'apophyse. Le test moins convexe des coquilles de Bachivillers est dû à une déformation par compaction post-sédimentaire. L'attribution du matériel thanétien à *Cyrtopleuropsis orbignyana* ne fait aucun doute.

Figs. 1-2. *Cyrtopleuropsis orbignyana* (Lévesque *in* Graves, 1847), valve droite de Cuise-la-Motte (Oise), Eocène inférieur (Cuisien), collection Lhomme, MNHN-LP, lot n° B50646. (Photo L. Merlette). x 2. **Figs. 3-4.** *Cyrtopleuropsis orbignyana* (Lévesque *in* Graves, 1847), valve gauche de Cuise-la-Motte (Oise). Eocène inférieur (Cuisien), collection Lhomme, MNHN-LP, lot n° B50646. (Photo L. Merlette). x 2. **Fig. 5.** *Cyrtopleuropsis orbignyana* (Lévesque *in* Graves, 1847), valve gauche de Bachivillers (Oise). Paléocène (Thanétien supérieur), collection Pons. (Photo P. Lozouet). grandeur nature, longueur: 97 mm., largeur: 29 mm. **Figs. 6-7.** *Cyrtopleuropsis orbignyana* (Lévesque *in* Graves, 1847), valve droite de Cuise-la-Motte (Oise). Eocène inférieur (Cuisien), collection Pacaud. ru: réflexion umbonale; cu: callosité umbonale; maa: empreinte du muscle adducteur antérieur; map: empreinte du muscle adducteur postérieur; a: apophyse; c: chondrophore. (Photo P. Lozouet). x 2. **Figs. 8-9.** *Cyrtopleuropsis orbignyana* (Lévesque *in* Graves, 1847), valve gauche de Cuise-la-Motte (Oise). Eocène inférieur (Cuisien), collection Pacaud. c: chondrophore. (Photo P. Lozouet). grandeur nature. **Figs. 10-11.** *Cyrtopleuropsis lescailloni* nov. sp., valve droite de Chamery (Marne). Eocène moyen (Lutétien moyen), holotype, MNHN-LP, lot n° R11583. (Photo P. Lozouet). x 1,5. **Fig. 12.** *Cyrtopleuropsis lescailloni* nov. sp., valve gauche de Chamery (Marne). Eocène moyen (Lutétien moyen), collection Pons. (Photo P. Lozouet). grandeur nature.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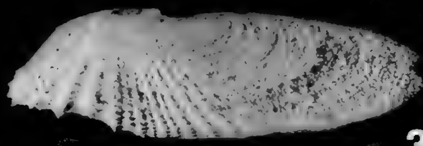
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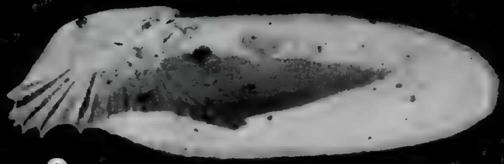
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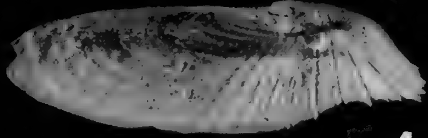
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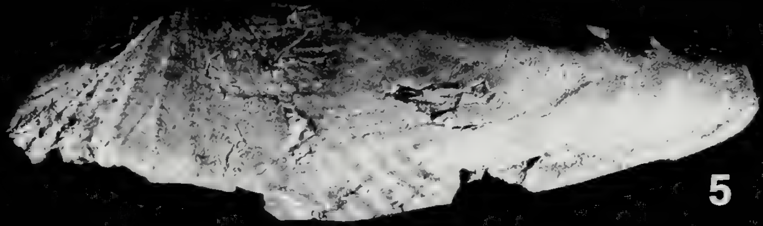
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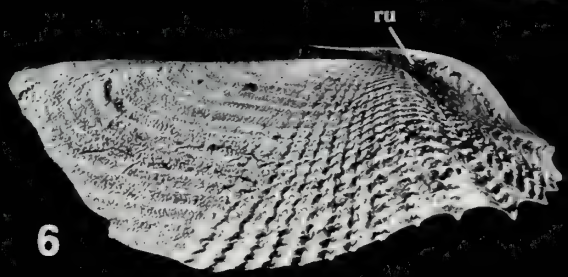

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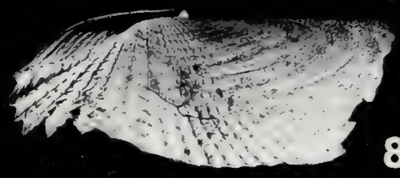
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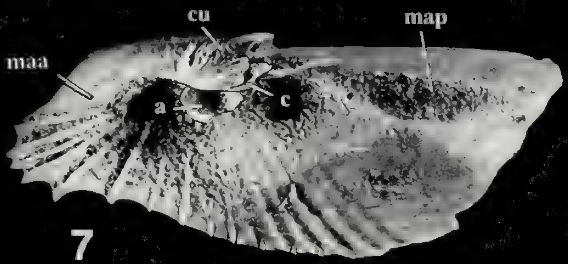

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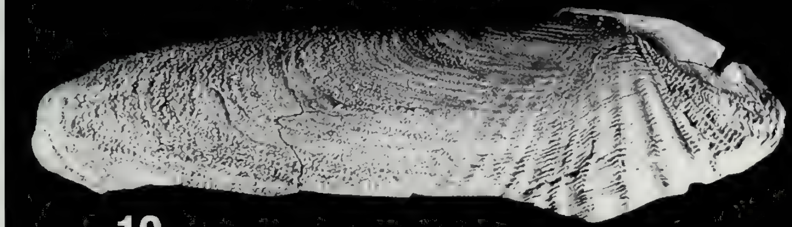
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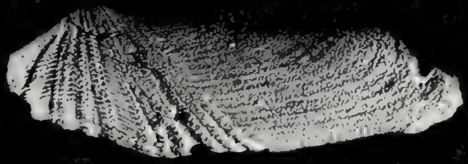
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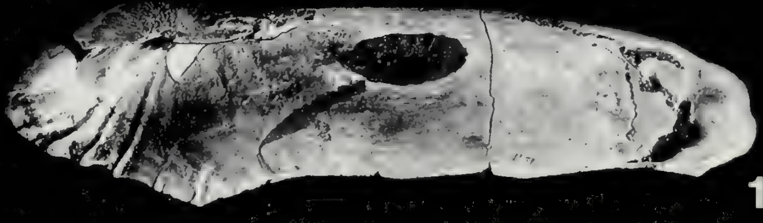
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Barnea cingulata Stinton, 1962, (Figs. 13) fondée sur un unique exemplaire (BMNH, lot n° LL14708) du Lutétien de Selsey (*Balanophyllia* Bed, Sussex, Angleterre) ne diffère de *C. orbignyana* que par un contour palléo-ventral nettement arrondi avant de se prolonger par un bord postérieur atténué. Les dernières côtes radiaires sont plus espacées dans la région médiane, cependant, l'échancrure antéro-ventrale ainsi que la sculpture radiaire sont analogues. JEFFERY & TRACEY (1997) considèrent *Barnea cingulata* comme synonyme de *C. orbignyana*, ce que je soutiens également. Le contour particulier du bord palléo-ventral n'est qu' un caractère individuel de l'holotype. J'ajouterai que *C. orbignyana* est signalé au Paléocène et à l'Eocène en Angleterre par NEWTON (1891), WRIGLEY (1930), STINTON (1962), TRACEY (1986) ainsi que TRACEY *& al.* (1996).

Cyrtopleuropsis lescailloni nov. sp.
(Fig. 10-12)

Synonymie: 1857 *Pholas Levesquei* Deshayes *partim, non* Watelet : 135 (*non* pl. 6, fig. 10-12).

Etage-type. Lutétien moyen (Eocène moyen).

Localité-type. Chamery, lieu-dit "Les Beurges" (Marne).

Derivatio nominis. Espèce dédiée à Michel Lescaillon.

Matériel-type. Holotype, Figs. 10-11 (MNHN-LP, lot n° R11583, récolte Lescaillon), valve droite.

Dimensions de l'holotype. Longueur: 75 mm., largeur: 18 mm.

Autre matériel. Chamery, lieu-dit "Les Beurges" (Marne): une valve droite (coll. Lescaillon); une valve gauche, Fig. 12 (coll. Pons); une valve gauche (coll. Boucher); Damery (Oise) *fide* DESHAYES; Grignon (Yvelines) *fide* DESHAYES.

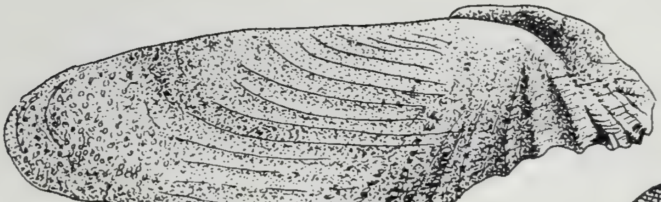
Diagnose. Coquille allongée, fortement inéquilatérale. Bord antérieur court, acuminé. Bord postérieur long et atténué. Valve épaisse et convexe. Bord antéro-ventral échancré et sinueux. Région antérieure de la surface dorsale ornée d'une sculpture radiaire composée de 15 à 17 côtes, bien marquées dans le test, s'interrompant au premier tiers de la longueur de la valve. Dans sa partie extrême, les 9 ou 10 premières côtes sont puissamment sculptées de chevrons imbriqués les uns dans les autres. Leur courbure importante applique une très nette convexité au bord antérieur. Elles sont largement espacées. Ces espaces sont ornés par de nombreuses lignes de croissance fines et serrées. Les côtes gravent leurs empreintes dans la surface interne sous forme de carènes lisses. Dans sa partie médiane, la sculpture radiaire de la surface dorsale est constituée de 6 à 7 côtes dont l'espacement est moindre et dont l'ornementation est plus faible que sur les côtes antérieures; leur inclinaison est plus importante et elles sont festonnées de petites écailles allongées. La surface interne est à peine marquée par ces côtes. Région postérieure de la surface dorsale parcourue par de nombreuses lignes de croissance sublamelleuses, régulières et bien marquées. De très nombreuses granulations couvrent cette surface, essentiellement dans la partie postérieure de la coquille.

L'impression du muscle adducteur postérieur, ovale, étroite et allongée est située très haut. Le sinus palléal est large, aigu en sa partie palléo-ventrale, il remonte très haut vers l'impression, petite et ovalaire, du muscle adducteur antérieur. Le bord cardinal est fortement retourné et enveloppe le crochet. La réflexion umbonale est non cloisonnée. La charnière est pourvue d'un solide chondrophore, aigu à son extrémité. L'apophyse est large et arrondie.

Comparaison. *C. lescailloni* se distingue de *C. orbignyana* par:

- une sculpture radiaire moins vigoureuse. Les espaces entre les costules sont nettement mieux festonnés par les lignes de croissance. Les côtes les plus proches du bord antérieur rejoignent la sinuosité de l'échancrure antéro-ventrale, donnant une nette convexité au bord antérieur (Fig. 12), tandis qu'elles sont fuyantes chez *C. orbignyana*, où pratiquement toutes les costules rejoignent le rostre antérieur (Fig. 8). L'ornementation rayonnante occupe chez *C. lescailloni* le tiers de la longueur totale, contre la moitié de la longueur chez *C. orbignyana*..

Fig. 13. *Barnea cingulata*, valve droite de Selsey (Sussex, Angleterre). Eocène moyen (Lutétien), holotype, BMNH, lot n° LL 14708. (d'après Stinton, 1963). x 2. **Fig. 14.** *Cyrtopleuropsis freyteti* (Plaziat, 1970), valve gauche de Montlaur (Aude). Sparnacien. (d'après Plaziat, 1970). x 2,5. **Fig. 15.** *Pholas aldrichi*, fragment de valve gauche de Bell's Landing (Alabama, Etats-Unis). Paléocène (Thanétien), holotype, USNM, lot n° 643735. (d'après de Gregorio, 1890). x 2. **Figs. 16-17.** *Cyrtopleuropsis alatoidea* (Aldrich, 1886), valve gauche de Gregg's Landing (Alabama, Etats-Unis). Paléocène (Thanétien), syntypes, USNM, lot n° 638792. (d'après de Gregorio, 1890). x 2. **Fig. 18.** *Cyrtopleuropsis alatoidea* (Aldrich, 1886), valve gauche de Gregg's Landing (Alabama, Etats Unis), Paléocène (Thanétien), syntype, PRI, lot n° 183. (d'après Harris, 1897). x 2. **Figs. 19-20.** Espèce-type du sous-genre *Cyrtopleura (s.str.), C. (s.str.) cruciger* (Sowerby, 1834). (d'après Turner, 1954). x 2. **Figs. 21-22.** Espèce-type du sous-genre *Cyrtopleura (Scobinopholas), C. (S.) costata* (Linné, 1758). (d'après Turner, 1954). x 0,7.



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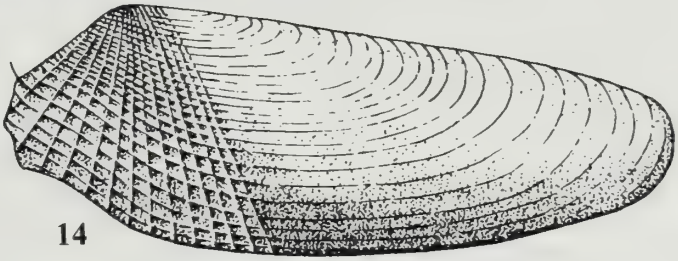

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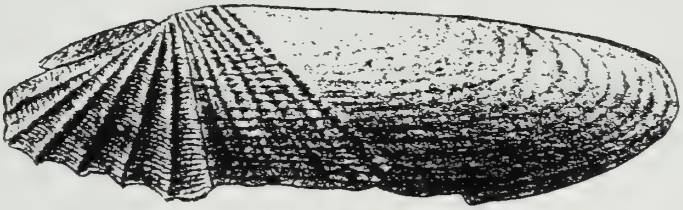

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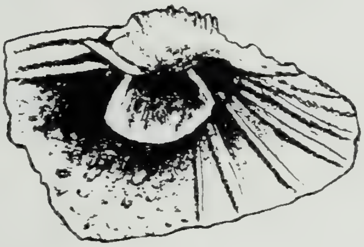

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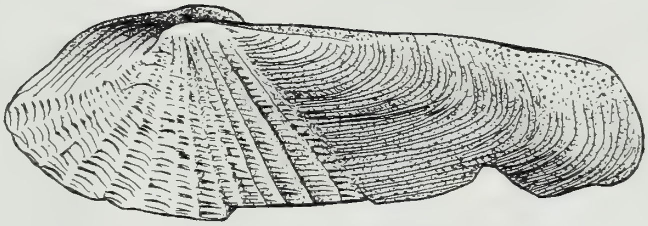

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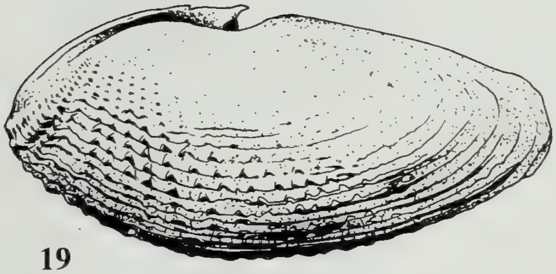

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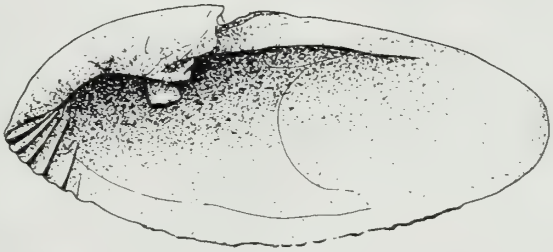

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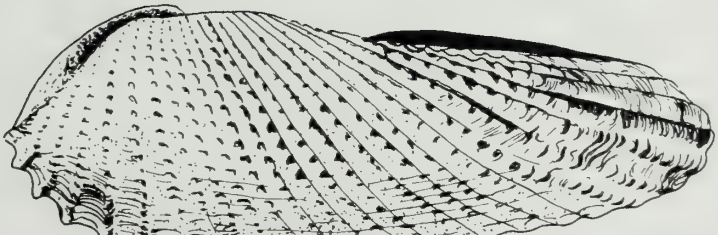

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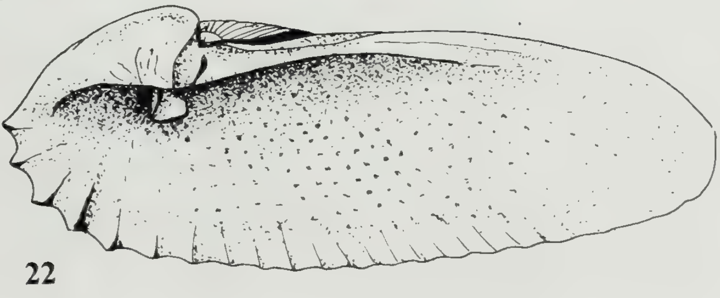

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- une surface dorsale parcourue par de plus nombreuses lignes de croissance. Elles festonnent les côtes antérieures de chevrons moins importants et nettement plus imbriqués les uns dans les autres. Le contour de l'échancrure antéro-ventrale est de ce fait nettement moins découpé que celui de *C. orbignyana*.
- un bord antérieur plus nettement arrondi, moins acuminé. Le contour de la réflexion umbonale enveloppant le crochet est arrondi tandis qu'il est sinueux chez *C. orbignyana*.
- un chondrophore plus fort, plus nettement bilobé sur la valve gauche. La lame inférieure est plus longue, plus aigüe.
- une face interne moins marquée par la sculpture radiaire où seules les côtes les plus proches du bord antérieur sont visibles. Les stries de croissance sublamelleuses ne se distinguent absolument pas à l'intérieur de la coquille comme on peut le voir chez *C. orbignyana*.
- une position plus haute et plus étroitement allongée de l'impression du muscle adducteur postérieur, placée pratiquement contre le bord palléal. La pointe aiguë du sinus palléal est plus étroite.

Cyrtopleuropsis freyteti
(Plaziat, 1970) nov. comb.
(Fig. 15)

1970 *Barnea freyteti* Plaziat : 61-62, fig. 41; pl. IX, fig. 15a-b.

Matériel-type. Syntypes, SE de Montlaur, Aude (coll. Plaziat, lots n° 1836 et n°1838); SW de Montlaur, Aude (coll. Plaziat, lot n° 1839); NW de Villemagne, Aude (coll. Plaziat, lot n° 1840).

Distribution. Yprésien (Sparnacien, Eocène inférieur).

Dimensions de l'exemplaire figuré (Syntype). Longueur: 34 mm.; largeur: 11 mm.

Observations. Cette espèce, contemporaine de *Cyrtopleuropsis orbignyana* (Sables sparnaciens de Sinceny, Aisne) s'en écarte toutefois par un allongement moins important, par un nombre de côtes moindre (12), et par l'inclinaison plus faible des côtes postérieures. L'ornementation rayonnante n'occupe seulement que le tiers de la longueur totale. Les coquilles ne sont pas isolées mais soudées à des plaquettes de calcaires bioclastiques et ne montrent pour la plupart que leur face externe. Les lots n° 1839 et 1840 montrent cependant leur face interne mais la charnière nous est inconnue et je ne peux donc discuter ni du chondrophore ni de l'apophyse; cependant les caractères morphologiques de la face dorsale de cette espèce, la sinuosité du bord antéro-ventral ainsi que la projection du bord antérieur, confirment l'appartenance de *Barnea freyteti* au genre *Cyrtopleuropsis*.

Cyrtopleuropsis alatoidea
(Aldrich, 1886) nov. comb.
(Fig. 15-18)

1886 *Pholas alatoidea* Aldrich : 36, pl. 4, fig. 9a-c.

Synonymie.

1848 *Pholas Roperiana* Tuomey : 153. *nomen nudum*.
1890 *Pholas Aldrichi* de Gregorio : 237, pl. 38, fig. 17.
1893 *Barnea alatoidea Aldrichi* (de Gregorio) - Cossmann : 5.
1965 *Pholas sp.* Palmer & Brann : 266.

Autres références.

1890 *Pholas alatoidea* Aldrich - de Gregorio : 237, pl. 38, fig. 15-16.
1893 *Barnea alatoidea* (Aldrich) - Cossmann : 5.
1897 *Pholas alatoidea* Aldrich - Harris : 69, pl. 13, fig. 15-15a.
1899 *Pholas alatoideus* Aldrich - Harris & Veatch : 304, pl. 53, fig. 12.
1960 *Pholas alatoidea* Aldrich - Brann & Kent : 686.
1965 *Pholas alatoidea* Aldrich - Palmer & Brann : 265.

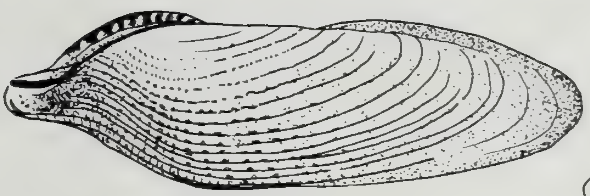
Matériel-type. Syntypes, Gregg's Landing, Alabama (Etats Unis): 2 valves gauches, dont une incomplète (USNM, lot n° 638792); Bell's Landing, Alabama (Etats Unis): 1 valve gauche incomplète (holotype du *Pholas aldrichi*, USNM, lot n° 643735).

Autre matériel. Gregg's Landing, Alabama (Etats Unis): 1 valve gauche et 1 valve droite incomplète (PRI, lots n° 183 et 184); Sabinetown, Texas (Etats Unis): " *Pholas sp.* " matériel perdu.

Distribution. Thanétien (Tuscahoma Formation et Sabinetown Formation, Paléocène).

Dimensions. Valve gauche syntype (Fig. 16) : Longueur: 50 mm; largeur: 14 mm.

Figs. 23-24. Espèce-type du sous-genre *Pholas (s.str.)*, *P. (s.str.) dactylus* Linné, 1758. Port-la-Nouvelle, Aude (coll. Pacaud). grandeur nature. **Figs. 25-26.** Espèce-type du sous-genre *Pholas (Monothyra)*, *P. (M.) orientalis* Gmelin, 1791. (d'après Turner *in* Moore, 1969). x 1. **Figs. 27-28.** Espèce-type du sous-genre *Pholas (Thovana)*, *P. (T.) campechiensis* Gmelin, 1791. (d'après Turner, 1954). x 0,5. **Figs. 29-30.** Espèce-type du sous-genre *Barnea (s.str.)*, *B. (s.str.) candida* (Linné, 1758). Port-la-Nouvelle, Aude (coll. Pacaud). x 2. **Figs. 31-32.** Espèce-type du sous-genre *Barnea (Anchomasa)*, *B. (A.) parva* (Pennant, 1777). (d'après Turner, 1954). x 1. **Figs. 33-34.** Espèce-type du genre *Zirfaea*, *Z. crispata* (Linné, 1758). (d'après Turner, 1954). x 1,5.



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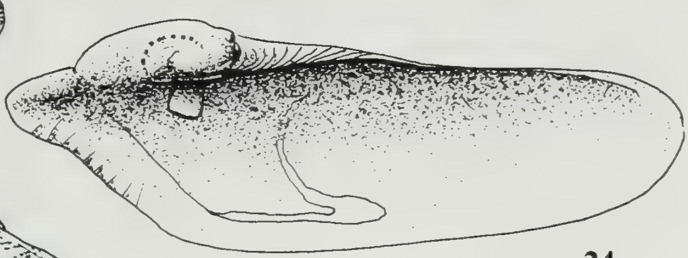

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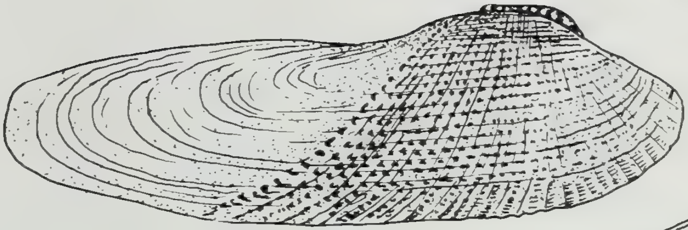

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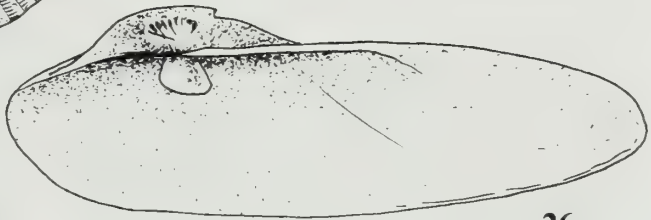

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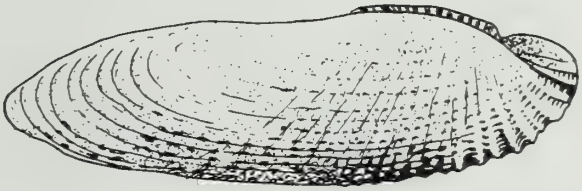

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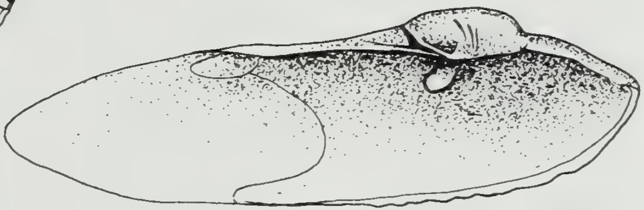

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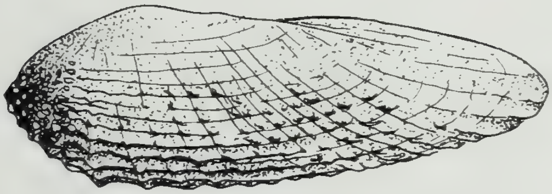

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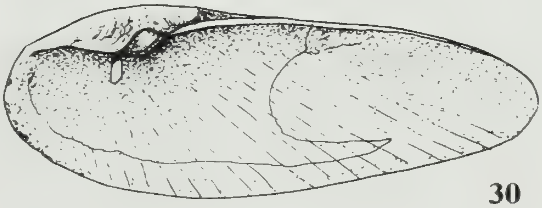

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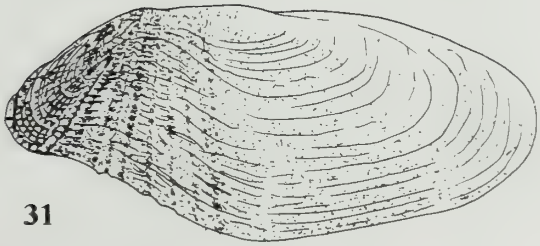

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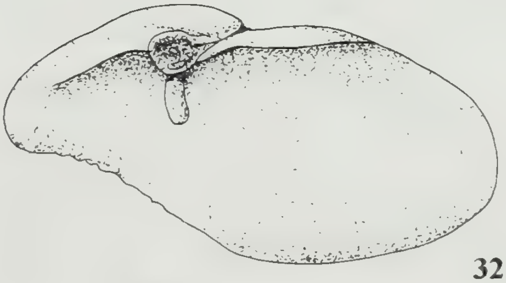

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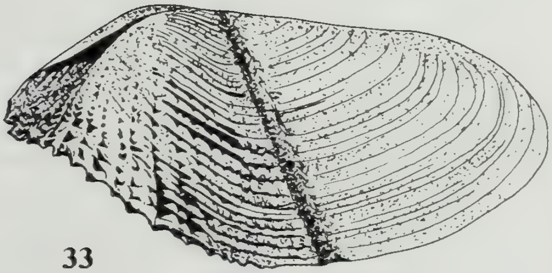

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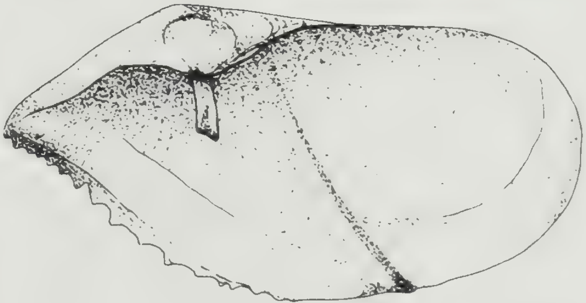

34

Observations. *Pholas alatoidea* Aldrich, 1886 du Thanétien de Gregg's Landing (Alabama, Etats Unis) appartient comme *C. orbignyana, C. freyteti* et *C. lescailloni*, au genre *Cyrtopleuropsis* par ses caractères morphologiques, par la forme de son apophyse et par la présence à la charnière d'un chondrophore. En outre, Harris (1897) figure une autre valve gauche (Fig. 18) provenant de la même localité, et sur laquelle on distingue nettement de nombreuses granulations couvrant la partie postérieure de la coquille. *Cyrtopleuropsis alatoidea* diffère de *C. orbignyana* par son bord antérieur moins acuminé, sans échancure antéro-ventrale nette. Les lignes de croissance festonnent les côtes antérieures de petites écailles, le contour antéro-ventral est de ce fait nettement moins découpé que celui de *C. orbignyana*. L'espèce américaine se rapproche bien plus de *C. lescailloni* par son extrémité antérieure non rostrée, par son échancrure antéro-ventrale peu marquée. Mais l'orientation des côtes les plus proches du bord antérieur est différente: projetées vers l'extrémité antérieure chez *C. alatoidea*, les côtes rejoignent la sinuosité de l'échancrure antéro-ventrale chez *C. lescailloni*. L'ornementation rayonnante occupe seulement le tiers de la longueur totale chez *C. lescailloni* et la moitié chez *C. alatoidea*. Une des figures de De Gregorio (1890) montre un chondrophore étroit remontant vers la callosité umbonale (Fig. 17), alors qu'il est projeté vers l'intérieur de la coquille chez *C. orbignyana* et chez *C. lescailloni*. *Pholas aldrichi* de Gregorio, 1890 (Fig. 15) du Thanétien de Bell's Landing (Alabama, Etats-Unis), fondé sur un fragment de la région antérieure, est tout à fait semblable à *C. alatoidea*.

Pour toutes ces raisons, je considère *C. alatoidea* comme une espèce distincte des espèces du Bassin Anglo-parisien. Elle est toutefois contemporaine de *C. orbignyana*; les unités lithostratigraphiques américaines "Bells Landing Marl Member" et "Greggs Landing Marl Member" , de la Tuscahoma Formation, sont actuellement attribuées au Thanétien (Siesser & *al.*, 1985).

CONCLUSIONS

Cyrtopleuropsis orbignyana, *C. freyteti*, *C. lescailloni* et *C. alatoidea* ne sont connues qu'au Paléogène inférieur du Nord de l'Atlantique. Elles ont en commun un bord antérieur fortement ornementé, un rostre antérieur bien individualisé, une sculpture radiaire s'interrompant dans la région médiane des valves, des granulations sur la surface dorso-postérieure, une apophyse arrondie et surtout une échancrure antéro-ventrale sinueuse. Les espèces actuelles et fossiles de *Cyrtopleura* et de *Scobinopholas* appartiennent à un groupe très voisin qui diffère par l'absence d'une échancrure antéro-ventrale nette, par une atténuation progressive de l'ornementation rayonnante qui se poursuit au-delà du milieu de la longueur et par la forme de l'apophyse, plus étirée chez *Cyrtopleura* (voir tableau 1).

D'après mes observations, l'existence de *Barnea* et de *Pholas (Monothyra)* dès le Crétacé (Turner, 1954; Turner *in* Moore, 1969) doit être remise en question. Je n'ai pas en effet pu observer la présence de ces deux genres dès le Mesozoïque.

Stephenson (1952) a décrit une espèce du Cénomanien (Crétacé sup.) de Cook County et de Grayson County de la "Woodbine Formation" (Texas, Etats Unis), *Pholas? scaphoides*. Je ne connais cette espèce que d'après les figures des faces externes qu'en donna l'auteur, ainsi que la figure reproduisant l'holotype donnée par Kennedy (1993). On ne peut en préciser le statut générique, ne distinguant ni un éventuel cloisonnement alvéolaire de la réflexion umbonale (brisée?) ni l'intérieur des valves. Kennedy (1993, p. 398) classe *Pholas scaphoides*, ainsi qu'une nouvelle espèce du Coniacien et du Santonien (Crétacé sup.) du Nord de la Californie, dans le genre *Barnea* (*Anchomasa*). Son choix est motivé uniquement sur l'apparente absence de cloisonnement alvéolaire de la réflexion umbonale. Kelly (1988), dans son inventaire des Pholades mésozoïques, considère *P. scaphoides* comme le plus ancien Pholadinae et rapporte cette espèce au genre *Pholas* (*Monothyra*). Les faces externes de *Pholas scaphoides* et de *Barnea* (*Anchomasa*) *saulae* Kennedy, 1993 montrent une ornementation radiaire dépassant la mi-longueur des valves ainsi qu'une très nette échancrure antéro-ventrale. Dartevelle & Freinex (1957) rapportèrent à *Pholas scaphoides* un moule externe de petite dimension et un fragment plus grand de moule interne provenant des niveaux crétacés du Congo (Afrique). Ces deux espèces, dont les caractères morphologiques des faces externes sont assez comparables à ceux de *Pholas (s. str.)* et de *Cyrtopleuropsis*, restent de classement douteux. Elles appartiennent vraisemblablement au même genre, toutefois le rattachement au genre *Barnea* (*Anchomasa*) n'est pas convaincant.

Pholas pectorosa Conrad, 1852, espèce-type du genre *Clavipholas* Conrad, 1868, a été décrit du Crétacé supérieur des Etats Unis (Stephenson, 1941). Toutefois, la possible fermeture du bord antérieur par un callum(Turner *in* Moore, 1969) chez *Clavipholas pectorosa* semble jeter un doute sur l'assimiliation de ce genre à la sous-famille des Pholadinae et serai probablement plus à sa place parmi les Martesiinae. On pourra ainsi noter les affinités de cette espèce avec *Pholas petrosa* Conrad, 1842. L'exemplaire figuré par Clark (1896) de l'Eocène du Maryland (Etats Unis) montre un galbe et une ornementation tout à fait semblable à *Clavipholas pectorosa*. Palmer & Brann (1965) rapportent *Pholas petrosa* au genre *Phenacomya* Dall, 1898. Ce genre est actuellement considéré comme synonyme du Martesiinae *Eutylus* Vincent, 1891. Ceci me conduit, dans l'ignorance des caractères internes des valves de l'espèce du Crétacé, au vu de sa morphologie et de ses affinités, à envisager de rattacher cette dernière plutôt aux Martesiinae.

Il ressort donc que *Cyrtopleuropsis* est le plus ancien Pholadinae décrit du Cénozoïque (tableau 2). *Pholas scaphoides* Stephenson, 1953 et *Barnea (Anchomasa) saulae* Kennedy, 1993 sont les seules Pholadinae mésozoïques connus. A ma connaissance, hormis *Zirlona increnata* (Marwick, 1929) du "Duntroonian" (Oligocène supérieur, voir BEU & MAXWELL, 1990) de Nouvelle Zélande, aucun autre Pholadinae n'a été décrit de l'Oligocène. La présence de *Cyrtopleuropsis alatoidea* (Aldrich, 1886) dans le Paléocène de l'Alabama et du Texas marque ainsi le premier jalon d'un groupe qui, sur les côtes américaines, évoluera vers celui de *Cyrtopleura-Scobinopholas*. Au Miocène, *Cyrtopleura (Scobinopholas) arcuata* (Conrad, 1841) est décrite de Nansemond River près de Suffolk en Virginie. CAMPBELL (1993) la signale également dans les sédiments miocènes de Yorktown, de Smithfield et de Chuckatuck en Virginie. DALL (1898) et HANNA (1926) signalent la présence de *C. (Scobinopholas) costata* (Linné, 1758) au Pliocène de Caloosahatchie marls en Floride et à Coyote Mountain en Californie. DALL (1898) signale *C. (S.) costata* au Pléistocène dans le Massachusetts, dans le Maryland et en Floride.

Actuellement, l'aire de distribution de *Cyrtopleura (s. str.)* est restreinte aux côtes du Mexique, du Costa Rica et du Panama. Celle de *C. (Scobinopholas)* est plus étendue; elle comprend, sans discontinuité, les côtes du Massachussets jusqu'aux côtes du Texas. *C. (Scobinopholas)* est également signalé sur les côtes brésilienne, uruguayenne et argentine.

Le tableau 2 montre donc la répartition stratigraphique des genres de la sous-famille des Pholadinae, l'echelle chronostratigraphique utilisées est celle proposée par ODIN & ODIN (1990).

REMERCIEMENTS. Je tiens à remercier Steve Tracey et Jean-Claude Plaziat pour les informations qu'ils m'ont apportées durant l'élabortion de cette note; Michel Lescaillon, Jacques Pons et Pascal Boucher pour le prêt de leur matériel; Didier Merle et le Pr. Agnès Lauriat-Rage pour la relecture du manuscrit. Je remercie également le Pr. Lauriat-Rage qui m'a permis de consulter les collections du Laboratoire de Paléontologie (MNHN-LP), Mme Denise Pajaud pour m'avoir laissé consulter la collection Munier-Chalmas (UPMC), ainsi que Mme Suzanne Freneix (MNHN-LP) pour les informations sur les faunes crétacées qu'elle m'a apportées. Je remercie aussi Pierre Lozouet (MNHN-BIMM) ainsi que Lionel Merlette (MNHN-LP) pour les clichés photographiques.

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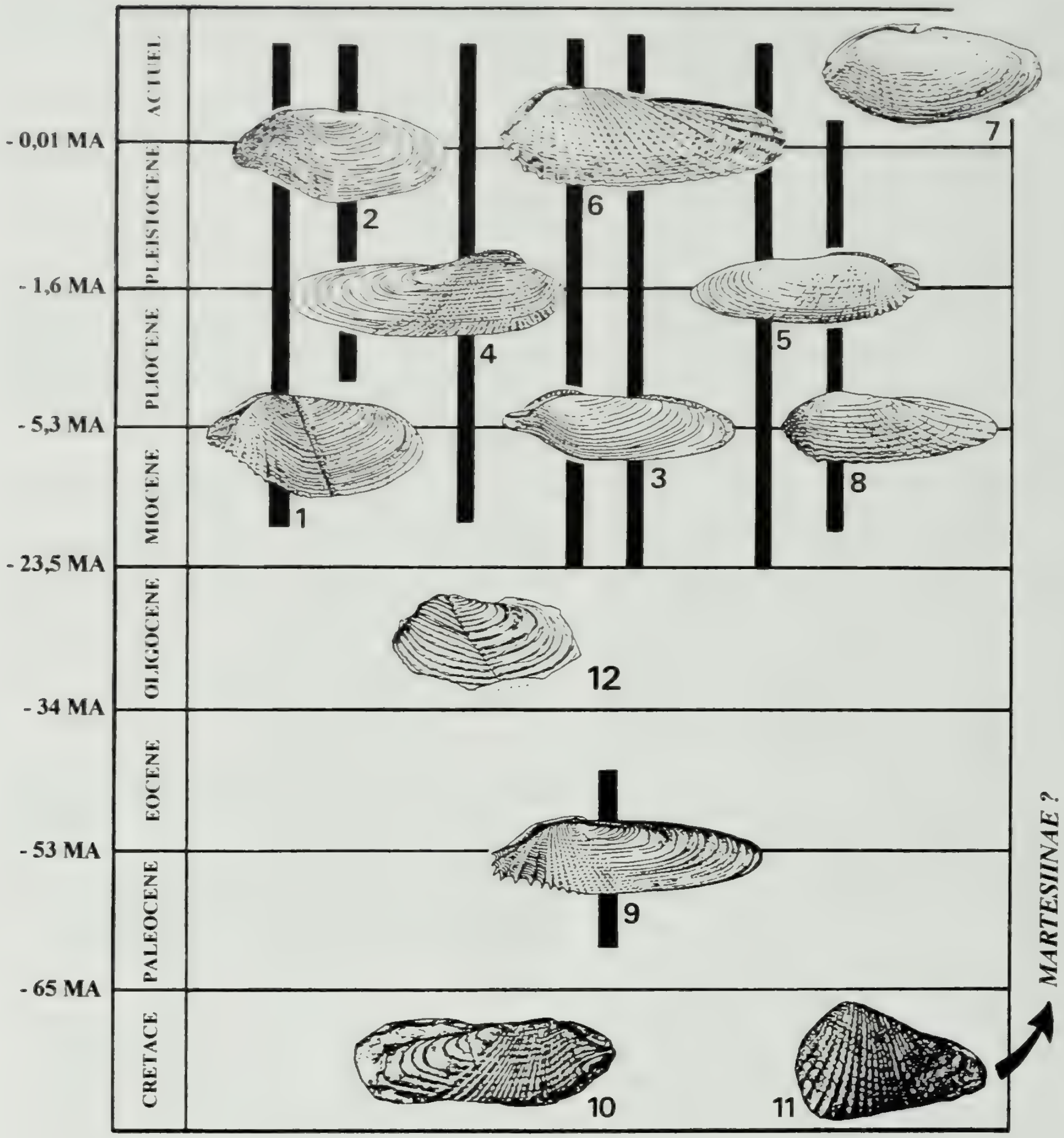

Tableau 2. Distribution stratigraphique de *Cyrtopleuropsis* et des genres voisins de Pholadinae: **1**, *Zirfaea* Leach *in* Gray, 1842; **2**, *Barnea (Anchomasa)* Leach, 1852; **3**, *Pholas (s.str.)* Linné, 1758; **4**, *Pholas (Thovana)* Gray, 1847; **5**, *Pholas (Monothyra)* Tryon, 1862; **6**, *Cyrtopleura (Scobinopholas)* Grant & Gale, 1931; **7**, *Cyrtopleura (s.str.)* Tryon, 1862; **8**, *Barnea (s.str.)* Leach *in* Risso, 1826; **9**, *Cyrtopleuropsis* nov. gen.; **10**, *Pholas an Cyrtopleuropsis ?* (*?Pholas scaphoides* Stephenson, 1952); **11**, *Clavipholas* Conrad, 1868; **12**, *Zirlona* Finlay, 1930.

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Description of a new species *Ischnochiton dolii* sp. nov. (Polyplacophora: Ischnochitonidae) from Civitavecchia, Italy

Richard A. VAN BELLE[1] and Bruno DELL'ANGELO[2]

[1] Scientific Collaborator, Koninklijk Belgisch Instituut voor Natuurwetenschappen,
Vautierstraat 29, B-1000 Brussels, Belgium
[2] Via Mugellese 66D, 59100 Prato, Italy

KEYWORDS. Polyplacophora, Ischnochitonidae, *Ischnochiton dolii* sp. nov., Italy.

ABSTRACT. *Ischnochiton dolii* sp. nov. is described. It is compared with all recent Mediterranean and northeastern Atlantic *Ischnochiton* species, and with the European fossil species from the Pliocene and the Miocene.

RESUME. *Ischnochiton dolii* sp. nov. est décrit et comparé à tous les *Ischnochiton* récents de la Méditerranée et du nord-est de l'Océan Atlantique, et aux espèces fossiles européennes du Pliocène et du Miocène.

INTRODUCTION

On June 1991, a Roman jar (=dolium ; IV century B.C.) was found in the Tyrrhenian Sea, off Civitavecchia, at a depth of 550 meters (Tringali & Ardovini, 1993). In the muddy contents 333 valves (69 head, 228 intermediate and 36 tail) were found of a possibly subfossil Polyplacophora species which proved to be new to science.

SYSTEMATICS

Family **ISCHNOCHITONIDAE** Dall, 1889
Subfamily **Ischnochitoninae**
Genus *Ischnochiton* Gray, 1847.

Type species : *Chiton textilis* Gray, 1828, SD Gray, 1847.

Ischnochiton dolii sp. nov.
Figs 1-5

Type material. Off Civitavecchia, -550 m, 333 valves : holotype, 3 x 7.5 mm (Fig. 1) + 5 paratypes in Museo di Zoologia of the Bologna University (holotype reg. no 11302, paratypes reg. no 11303) , other paratypes in Institut Royal des Sciences Naturelles de Belgique (4 valves, reg. no IG 28523), Museum National d'Histoire Naturelle, Paris (3 valves), R. Ardovini coll. (138 valves), F. Giovini coll. (80 valves), B. Dell'Angelo coll. (90 valves, reg. no P151F/01), R.A. Van Belle coll. (12 valves, reg. no F1003a).

Tuscan Archipelago, -70/100 m : 1 intermediate valve, 2.2 x 5.5 mm (B. Dell'Angelo coll. reg. no L15/01).

Type locality. Tyrrhenian Sea, off Civitavecchia, Italy, -550 m.

Diagnosis. Dimensions of largest valves : head valve 3.5 x 7 mm, intermediate valve 3 x 7.5 mm, tail valve 4 x 6.5 mm. Considering the size of these valves and the fact that all *Ischnochiton* species are oval to elongate oval, one can assume that *I. dolii* was an animal of medium size (up to about 20 mm long), rather elevated (jugal angle 85-110°), carinated with the side slopes straight, the valves not beaked. Colour of tegmentum dark brown, variously blotched and/or streaked with white.

Description. Head valve (Fig. 2) semicircular, front slope straight to very weakly concave, posterior margin widely V-shaped, deeply notched in the middle, tegmentum sculptured with rather flat, subgranulose radiating ribs, 17-26 near apex, splitting up to more than double that number near periphery of valve, interstices very narrow, ribs concentrically crossed by numerous growth lines. Valve II pentagonal, other intermediate valves (Figs 1, 4) broadly rectangular, front margin obtusely angular, straight and slightly slanting at both sides of jugal angle, side margins weakly convex, hind margin straight, mucro inconspicuous, lateral areas moderately elevated, sculptured like head valve, 4-5 radiating ribs, in some valves becoming obsolete towards side margin, central area with 13-19 longitudinal sulci (Fig. 5) on both sides of the smooth, wedge-shaped jugum, the 3-4 innermost sulci forwardly converging towards jugum, intervening ribs rather flat, slightly wider than sulci. Tail valve (Fig. 3) depressed, short, about twice as wide as long, front margin broadly angular like in intermediate valves, hind margin less than semicircular, mucro slightly antemedian, little raised, antemucronal area sculptured like central area of intermediate valves, postmucronal area with 18-20 radiating, flattish ribs, crossed by rather deep concentric grooves, in some valves this sculpture becomes indistinct near the mucro.

Articulamentum whitish, apophyses wide, short, evenly rounded, jugal sinus shallow, relatively narrow, weakly convex, insertion plates short, slit formula 9-10/1/7-8 (one intermediate valve has a second slit on one side), slits inequidistant, upper area of teeth grooved, eaves very narrow.

Distribution. Only known from the type material.

Remarks. As the subgeneric division of *Ischnochiton* s.l. is partly based on characteristics of the perinotum (here lacking), a subgeneric assignment for *I. dolii* is impossible.

A similar remark equally applies to all fossil *Ischnochiton* species.

Etymology. The specific name refers to the Roman jar (= dolium) in which the valves have been found.

Discussion. Comparing the recent European *Ischnochiton* species with *I. dolii*, we conclude that the latter differs from them all.

I. (Stenosemus) albus (Linnaeus, 1767), an Atlantic species, has the tegmentum of all valves uniformly microgranulose, smooth and glossy to the naked eye.

Apart from the tegmental colour and the always present, wavy concentric lirae on end valves and lateral areas of intermediate valves, *I. (Simplischnochiton) rissoi* (Payraudeau, 1826), common in the Mediterranean Sea, has a much greater number of longitudinal riblets on the central areas.

I. (Stenosemus) exaratus (G.O. Sars, 1878), an Atlantic deep water species, differs by the uniformly dirty white to yellowish tegmental colour, the weaker sculpture and especially, on the central areas, the longitudinal sulci which do not reach the posterior margin of the valve.

I. (Simplischnochiton) obtusus Carpenter *in* Pilsbry, 1893, described from Portugal, has the lateral areas more strongly raised, only 10 longitudinal sulci on the pleural areas, and the mucro of the tail valve median and prominent.

I. dolii seems closest related to *I. (Stenosemus) vanbellei* Kaas, 1985, known from the white coral banks of the Ligurian Sea, but that species has only 16 non splitting, radiating ribs on the head valve, 2 ribs (3-4 in valve II) on the lateral areas of the intermediate valves, and only 7-9 longitudinal sulci on either side of the jugum.

As the correct geological age of *I. dolii* cannot be established with any degree of certainty, *I. dolii* needs to be compared with European Pliocene and Miocene *Ischnochiton* species too.

Both *I. anserinus* Laghi, 1977, from the Pliocene of the Modena Basin, Italy, and *I. ulivii* Dell'Angelo & Forli, 1996, from the Pliocene of Pietrafitta, Italy, have a completely different sculpture, without longitudinal or radiating ribs.

I. rudolticensis Sulc, 1936, from the Miocene of the Vienna Basin, Austria, has a sculpture resembling that of *I. (S.) rissoi* and consequently cannot be conspecific with *I. dolii*.

I. korytnicensis Baluk, 1971, from the Miocene of the Holy Cross Mountains, Poland, has undulating longitudinal ribs on central area of intermediate valves, and irregular nodular elevations, variable in outline, on lateral areas and end valves.

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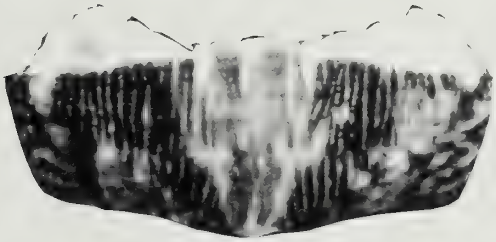

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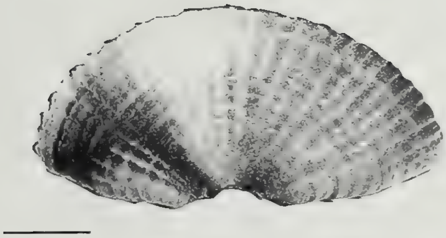

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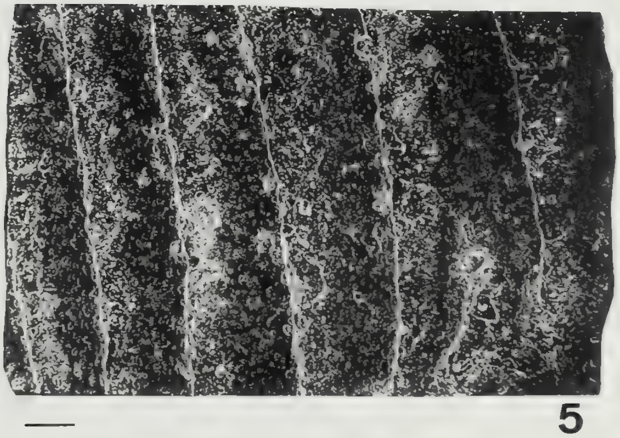

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Figs. 1-5. *Ischnochiton dolii* sp. nov. **Fig. 1.** Holotype, 3 x 7.5 mm, Bologna Museum 11302 (photo E. Ulivi). **Figs. 2-5.** Paratypes, Bologna Museum 11303 (SEM photos C. Lombardi). **Fig. 2.** Head valve. **Fig. 3.** Tail valve. **Fig. 4.** Intermediate valve. **Fig. 5.** Detail of sculpture of pleural area of intermediate valve. Scales - 2-4 ; 1 mm ; 5 : 100 µm.

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The influence of physicochemical parameters on the distribution of dominant bivalve species in the ensenada do Baño (Ria de Ferrol) in Northwest of Spain

C. OLABARRIA [1], V. URGORRI [2] & J. S. TRONCOSO [3]

[1] Fac. Ciencias del Mar, Univ. Autónoma de Sinaloa, C/Paseo Claussen s/n, 82000 Mazatlán (Sinaloa), Mexico
[2] Depart. Bioloxía Animal, Fac. de Bioloxía. Universidade de Santiago, E-15706, Santiago (La Coruña), Spain
[3] Depart. de Recursos Naturais e Medio Ambiente, Fac. de Ciencias do Mar, Universidade de Vigo, Vigo, Spain

KEYWORDS. Bivalves, synecology, physicochemical parameters, Ría de Ferrol, Spain.

MOTS CLEFS. Bivalves, synécologie, facteurs physico-chimiques, Ría de Ferrol, Espagne.

ABSTRACT. This paper presents a synecological study of the dominant bivalve species in the Ensenada do Baño (Ría de Ferrol, NW Spain), and reports on relationships between the distribution of these species and physicochemical parameters (particle size, carbonate content, organic matter content, sorting coefficient and depth/ height with respect to tidal zero). We conclude that the most important factors governing species distribution are grain size and depth/height.

RÉSUMÉ. Une étude synécologique des bivalves dominants de l' Anse do Baño (Ría de Ferrol, NO Espagne) est présentée. Cette étude montre les relations entre leur distribution et les conditions physico-chimiques du milieu (granulométrie, teneur en carbonates et en matière organique, coefficient de sélection et profondeur). Cette étude a permis de mettre en évidence que les facteurs déterminant de la distribution des bivalves sont le gradient sédimentaire et la profondeur ou la hauteur par rapport au niveau 0 de la marée.

INTRODUCTION

In early studies on the biology of benthic faunas, an understanding of sedimentological parameters proved to be of utmost importance, due to their effect on the faunal composition of communities and to the close relationship between sediment variables and the ecological preferences of the different species. This is particularly true for infaunal species, which the nature of the sediment determines life style as well as trophic and reproductive habits.

In a number of studies, the primary goal has been to gather information on relationships between mollusc distributions and the physicochemical properties of the sediment. It has been observed that the relationship between mollusc distributions and the sedimentary environment is the result of a dynamic interdependence among physical, chemical and microbiological sediment factors (BADER, 1954). Important studies in this field include those of LANDE (1975), TUNBERG (1981) and CORNET (1985, 1986) on the distribution and ecology of bivalve communities of European Atlantic coast, and those of DRISCOLL & BRANDON (1973), FRANZ (1976), FRANZ & MERRILL (1980) on the American Atlantic coast in which benthic molluscan assemblages in relation to sediment were studied. Previous studies about distribution and ecology of molluscs of the coasts of northern Spain include those of FIGUERAS (1956), VIÉITEZ (1976), PLANAS & MORA (1984), LABORDA & MAZÉ (1987), MAZÉ & LABORDA (1988), BORJA (1988, 1991) and TRONCOSO & URGORRI (1992).

Despite of abundance of malacological studies on the Galician coasts, there is a scarcity of research on sinecology of molluscs. For that, we decided to extend the knowledge of this group, particularly in the Ría de Ferrol, where this group has been poorly studied. In the present study, we investigated relationships between bivalve distributions and physicochemical factors in the Ría de Ferrol. The study was carried out in the Ensenada de Baño (Baño Inlet), which contains a wide range of sediment types (including mud, muddy sand, shell gravel, coarse sand and maërl).

METHODS

The study area is located on the southern side of the Ría de Ferrol (NW Spain), between Punta do Faro da Palma (43°27'52"N; 08°16'49"W) and Punta Piteira (43°27'57"N; 08°15'37"W), and has an area of 0.5 km^2 and a maximum depth of 18 m (Fig. 1).

The inlet is oriented in direction NNE-SSW; the prevailing winds are southwesterlies for most of the year, except in summer when northeasterlies become dominant. The mean tidal range in the ria is 2,7 m, and tidal effects give rise to strong currents (up to 1,5 m/s in the ria's central channel). Outward movement of water from the ria provokes movement to the SE within the inlet, while movement into the ria provokes movement to the SSW within the inlet. These currents, which are stronger at the mouth of the inlet than at more distal points, are the dominant factor affecting sediment distribution within the inlet.

Mollusc were sampled between July 1991 and June 1992 at 40 intertidal and 35 subtidal stations (one sample per station). Sampling points were selected along 12 parallel transects drawn across the inlet at 100 m intervals, taking samples at the points that were judged by visual examination to show a change in nature, texture or substrate covering. In the subtidal zone, the samples were collected by scuba diving. At each point, a 0,25 m^2 square sample was taken, to a depth of approximately 20 cm, using a rectangular shovel. The tidal range at intertidal stations was 2.29 m. The intertidal samples were additionally collected at the ends of each transect and, in the inner intertidal zone, samples were also taken every 100 m along each transect (OLABARRIA *et al.*, 1996). All samples were subsequently wet-sieved through a series of sieves with 10, 2, and 0.5 mm mesh. Finally the sieved samples were transported to the laboratory to be sorted by the remounting technique (ROS, 1975).

Surface sediment samples were also collected from each sampling point, for granulometric analysis and for determination of organic matter and carbonate content by the method of GUITIÁN & CARBALLAS (1976) (Table 1).

For each species and each environmental factor, possible relationships between population density (number of individuals in the sample) and the level of that factor were investigated by Spearman rank correlation analysis (SOKAL & ROHLF, 1979) (Table 2).

RESULTS

Distribution of individual species with respect to sediment characteristics

The samples yielded a total of 7579 specimens of bivalves belonging to 52 species, of which 11 (*Mytilus edulis, Thyasira flexuosa, Mysella bidentata, Papillicardium papillosum, Parvicardium exiguum, Cerastoderma edule, Abra alba, Venus verrucosa, Dosinia exoleta, Venerupis senegalensis* and *Hiatella arctica*) represented 80.8% of the total, with *Mysella bidentata* being the most representative species (35.6%) (Table 3).

Mytilus edulis occurred most commonly in the intertidal zone (93.3%), of individuals, versus 6.7% in the subtidal zone reaching its highest densities in coarse sand bottoms located in the intertidal zone on the border of the inlet (Fig. 2A). The density of individuals in the intertidal zone was positively correlated with gravel, coarse sand, and carbonate contents, and negatively correlated with fine sand content (Table 2).

Thyasira flexuosa was found almost exclusively in the subtidal zone (99.4% of individuals), reaching its highest densities in the eastern area of the inlet (Fig. 2B), on fine sand bottoms with silt-clay contents of over 10% and organic matter contents of 1-2%. There was a strong positive correlation between the density of this species in the subtidal zone and fine sand and organic matter contents, and a strong negative correlation with coarse sand and carbonate contents (Table 2).

Mysella bidentata was the most abundant and widely distributed bivalve, with a broad distribution throughout the inlet and a large number of individuals in the subtidal zone (Fig. 2C). Correlation analysis did not reveal any relationship with physicochemical parameters in the subtidal zone, due to the widespread occurrence of this species on all types of bottom. In the intertidal zone, however, the density of this species correlated positively with coarse sand and gravel contents, and negatively with fine sand content (Table 2).

Papillicardium papillosum occurred most commonly in the subtidal zone (96.7% of individuals). The highest densities were those observed in the outer subtidal zone (Fig. 2D), dominated by coarse sand and medium sand bottoms with organic matter contents of less than 1% in most cases. The density of this species in the subtidal zone was positively correlated with coarse sand content and depth, and negatively correlated with fine sand content (Table 2).

Parvicardium exiguum was commonest in the intertidal zone (86.4% of individuals). The highest densities were found in the mid-intertidal zone where there is a *Zostera noltii* meadow (Fig. 3A). The density of this species in the subtidal zone showed a significant though weak positive correlation with medium and fine sand contents, and a significant negative correlation with gravel and carbonate contents. In the intertidal zone, the density of this species was negatively correlated with tidal height (Table 2).

Cerastoderma edule was present only in the intertidal zone, and reached its highest densities in the inner intertidal zone (Fig. 3B), where the bottoms are mostly medium and fine sand with organic matter content ranging between 0.5 and 1%. Correlation analysis did not reveal significant relationships with the physicochemical parameters, except for a negative correlation with tidal height (Table 2).

Abra alba was most frequent in the subtidal zone (84.5% of individuals). However, it was widely distributed in the inlet (Fig. 3C), being most common on bottoms with particle size smaller than 0.5 mm and organic matter content greater than 1%. The density of this species in the subtidal zone correlated positively with the sorting coefficient and less strongly with organic matter content, and negatively with coarse sand

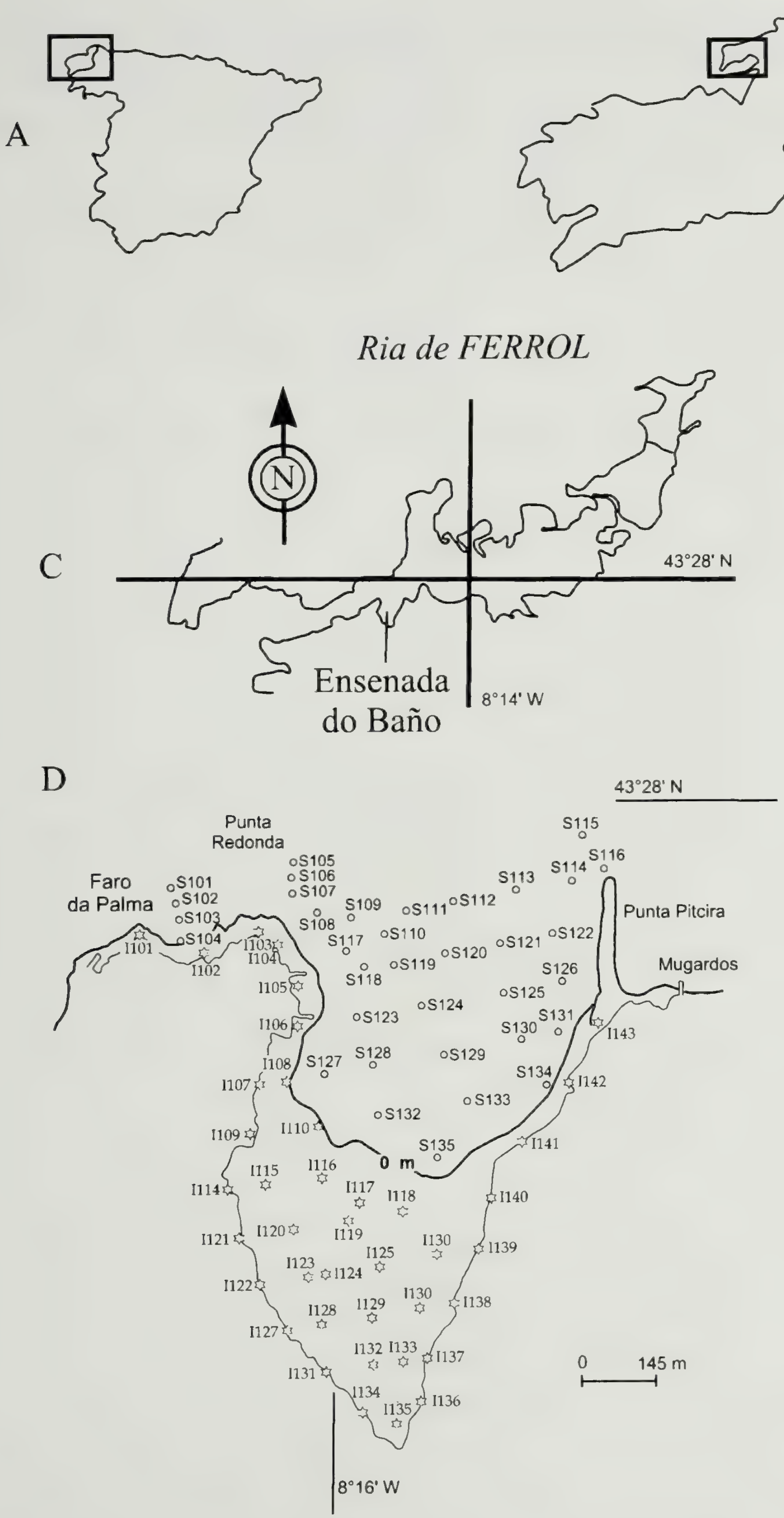

Fig. 1. Location of the study area and the sampling sites. A: Spain; B: Galicia; C: Ría de Ferrol; D: Ensenada do Baño.

content. In the intertidal zone, density showed a weak but significant positive correlation with silt-clay content (Table 2).

Venus verrucosa occurred largely in the subtidal zone (94.5% of individuals), and reached its highest densities on bottoms with coarse sediments and varying percentages of organic matter (Fig. 3D). The density of this species in the subtidal zone was negatively correlated with fine sand content. In the intertidal zone, however, a positive correlation was observed between the density of this species and both coarse sand content and the sorting coefficient (Table 2).

Dosinia exoleta occurred most commonly in the subtidal zone (96.8% of individuals), and reached its highest densities in the outer part of the inlet on coarse sand bottoms with variable organic matter content (0.4-1.7%) (Fig. 4A). The density of this species correlated positively with coarse sand content and to a lesser extent with carbonate content, and negatively with fine sand content (Table 2).

Venerupis senegalensis was slightly more frequent in the subtidal zone (61.8% of individuals), attaining its highest densities in the outer inlet. In the intertidal zone it was distributed homogeneously throughout the whole area. In both cases, it occurred on bottoms of varied physicochemical characteristics (Fig. 4B). In the intertidal zone, density was negatively correlated with tidal height (Table 2).

Site	Q_{50}	S-C	S_o	CA	OM	D/H	Site	Q_{50}	S-C	S_o	CA	OM	D/H
S101	1.02	10.2	2.4	30.2	0.4	10.25	**I103**	1.30	10.6	>2.5	19.6	0.6	0,80
S102	0.71	20.3	2.7	31.1	0.5	7.25	**I104**	1.30	1.6	1.8	20.6	0.4	0,21
S103	0.41	20.7	1.7	33.3	0.4	4.25	**I105**	0.32	5.4	1.6	9.4	0.7	1,75
S104	0.15	35.3	6.0	18.2	1	1.03	**I106**	0.65	2.5	2.6	12.9	0.4	0,74
S105	2.31	20.2	4.8	34.7	0.7	11	**I107**	0.65	4.7	2.5	2.6	0.5	0,52
S106	0.53	27	8.4	8.9	1	9	**I108**	0.40	4.8	1.9	2.1	0.5	00
S107	2.90	20.6	6.4	32.4	1.9	5	**I109**	>2	3.8	>1.6	1.7	0.6	0,55
S108	3.00	14.2	2.2	34.7	1.2	4.3	**I110**	0.80	5	3.7	8.6	2	1,13
S109	0.09	45.7	9.6	29.3	1.5	7.2	**I114**	1.80	1.5	>1.3	1.7	0.2	0,84
S110	1.90	11.5	2.7	32.9	0.7	13.2	**I115**	0.28	6.2	1.8	1	0.5	0,70
S111	0.18	36.9	0.2	32	1.7	13	**I116**	0.45	17.5	5.0	0.3	1.4	0,74
S112	0.25	31.9	21.7	13.8	1.1	17	**I117**	1.40	11.4	3.7	26.7	0.6	0,10
S113	0.44	7.7	2.5	13.8	0.9	17	**I118**	0.38	4.4	2.9	16.3	0.3	0,98
S114	0.11	44.6	20.9	21.3	1.4	14	**I119**	0.18	5.5	1.6	0.8	0.6	1,91
S115	0.85	11.4	2.0	34.7	0.4	15.5	**I120**	0.13	8.7	1.5	0.3	0.9	0,16
S116	0.49	12.8	1.7	34.7	0.6	11	**I121**	1.80	4.4	>2.5	0.8	0.9	1,30
S117	0.65	12.5	2.1	4.9	0.3	2	**I122**	0.12	15.9	1.5	1.7	1.4	0,91
S118	0.34	27.3	9.5	24.9	1.5	4	**I123**	0.16	6.5	1.9	0.3	0.6	0,94
S119	1.75	13.2	2.6	17.3	0.4	8	**I124**	0.13	10.9	1.4	0.2	0.8	0,08
S120	1.39	14.6	3.4	18.4	0.6	13	**I125**	0.11	10.7	1.4	0.3	0.8	0,27
S121	3.00	6	2.5	27.6	0.9	18	**I126**	0.14	5.6	1.3	1	0.4	0,57
S122	1.21	23.4	7.5	30.2	0.6	16	**I127**	0.32	10	2.3	0.9	0.5	0,80
S123	1.55	13.2	>2.3	16.4	0.4	5	**I128**	0.34	6.6	2.2	0.3	0.8	0,38
S124	1.40	11.4	>3.3	30.2	0.7	10	**I129**	0.15	3.5	1.4	0.9	1	0,81
S125	0.16	40	10.0	35.6	0.9	13	**I130**	0.13	9	0.3	0.3	1.2	0,92
S126	>2.00	7.7	>3.9	22.6	1.3	10	**I131**	0.24	27.7	4.3	0.9	0.5	1,03
S127	0.09	13.3	>1.8	2.2	1.8	1.2	**I132**	0.13	6.6	1.4	0.2	0.7	1,67
S128	1.55	5.4	>3.5	6.3	0.3	4.5	**I133**	0.13	7.6	1.4	0.3	0.9	1,45
S129	0.13	37.9	8.5	17.3	1.8	9.8	**I134**	0.11	5.4	1.3	0.2	0.9	1,78
S130	0.06	49.8	9	25.8	1.5	12	**I135**	0.26	4.7	1.5	1	0.5	1,78
S131	0.03	53.1	8.5	16.3	2	7.6	**I136**	0.19	4.7	1.7	0.2	0.4	1,05
S132	0.23	10.4	1.6	1.3	0.6	1.5	**I137**	0.12	11	1.4	0.2	0.9	1,63
S133	0.06	46	5.2	6.2	2	5.8	**I138**	0.18	5.5	3.7	0.2	0.8	1,20
S134	0.75	13.1	>3.5	19	0.9	6.4	**I139**	0.36	7	3.9	0.9	0.7	1,59
S135	0.19	17	1.7	0.9	0.4	2	**I140**	0.13	27.9	7.2	0.9	0.6	0,84
I101	>2	0.9	1.1	12	0.2	0.35	**I141**	0.90	5.5	3.0	4.3	0.7	0,68
I102	0.35	5.9	1.8	1.4	0.4	2.29	**I142**	0.32	4.7	1.6	24.9	0.4	0,96
							I143	0.36	9.7	3.6	14.3	0.8	0,78

Table 1. Characteristics of the sampling sites. Q_{50} : median particle size (mm); S-C : silt and clay contents (% w/w); S_o : sorting coefficient; CA : carbonate content (% w/w); OM : organic matter content (% w/w); D : depth (m) with respect to tidal zero (subtidal sites); H : height (m) with respect to tidal zero (intertidal sites).

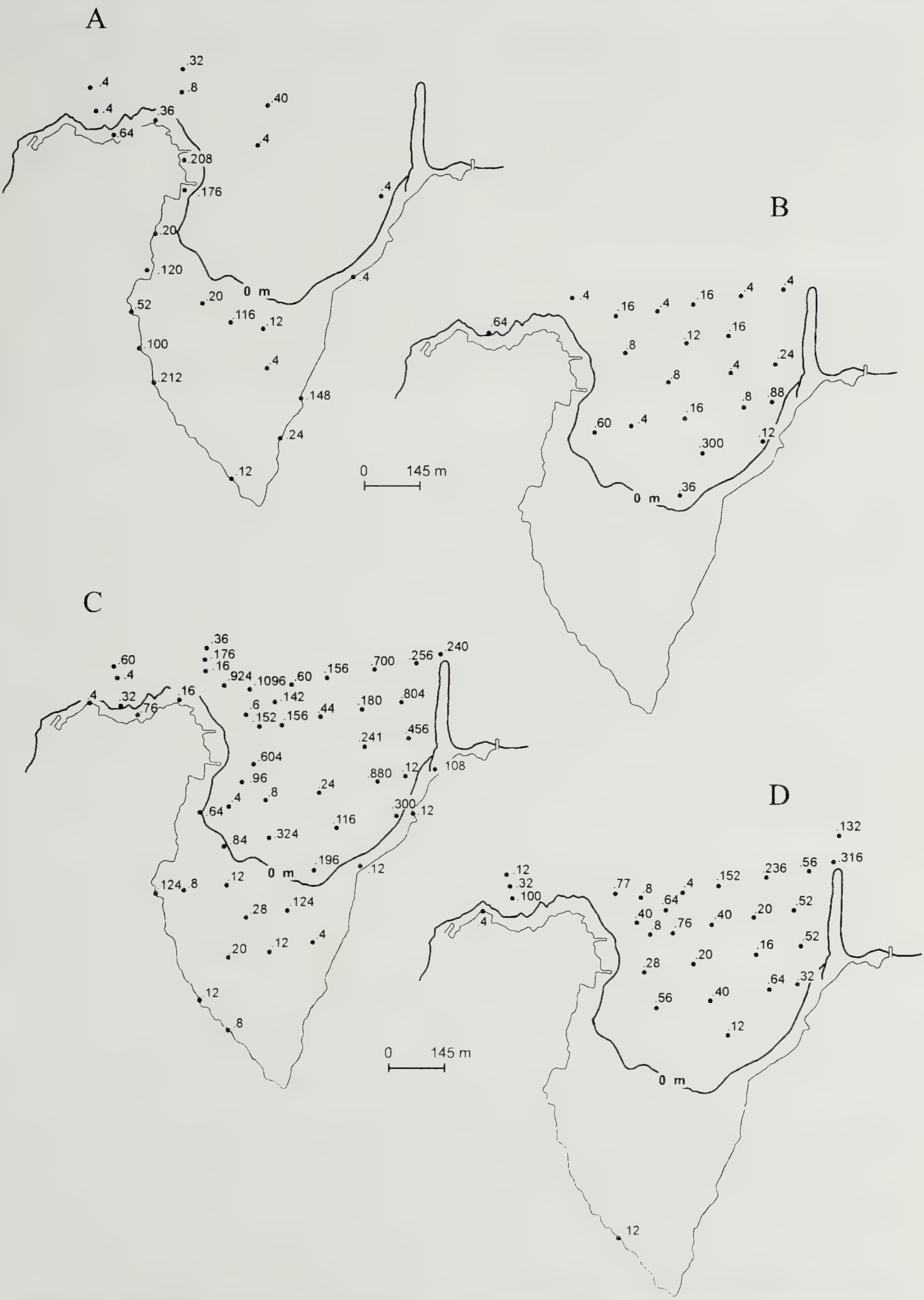

Fig. 2. Estimated densities (individuals per m^2) of *Mytilus edulis* (A), *Thyasira flexuosa* (B), *Mysella bidentata* (C) and *Papillicardium papillosum* (D) at sites at which that species was found

Hiatella arctica was likewise slightly more frequent in the subtidal zone (65.5% of individuals), largely occurring on bottoms with a particle size greater than 0.5 mm, both in the subtidal and intertidal zone (Fig. 4C). The density of this species in the subtidal zone showed a slight positive correlation with gravel content and depth. In the intertidal zone the density of this species correlated positively with coarse sand, carbonate and gravel contents, and negatively with organic matter and fine sand contents (Table 2).

Among species relationships

In the subtidal zone, extensive overlap was observed among the distribution of *Hiatella arctica*, *Venus verrucosa* and *Venerupis senegalensis* (Fig. 5A), and similarly among the distribution of *Abra alba*, *Thyasira flexuosa* and *Mysella bidentata* (Fig. 5B), though note that the latter was very common throughout the subtidal zone. *Thyasira flexuosa* and *Dosinia exoleta* were not found together (Fig. 5B), since *D. exoleta* occurs on infralittoral gravel and *T. flexuosa* on muddy sands or muds. *Papillicardium papillosum* showed high densities (up to 150 individuals/m^2) on the deepest bottoms dominated by coarse sands.

In the intertidal zone, extensive overlap was observed between *Hiatella arctica* and *Venus verrucosa* and between *Parvicardium exiguum* and *Venerupis senegalensis* (Fig. 5A). *V. verrucosa* and *H. arctica* occurred in the same types of habitat (coarse sands and gravels), whereas *P. exiguum* and *V. senegalensis* both occurred on a wide range of bottom types. *Cerastoderma edule* occurred most commonly at intermediate tidal levels, with the highest densities at

SUBTIDAL									
Species	**G**	**CS**	**MS**	**FS**	**SC**	**OM**	**CA**	**S_o**	**D**
Mytilus edulis	0.103 ^{NS}	-0.004 ^{NS}	-0.060 ^{NS}	-0.311 ^{NS}	-0.028 ^{NS}	0.033 ^{NS}	0.143 ^{NS}	-0.238 ^{NS}	0.048 ^{NS}
Thyasira flexuosa	**-0.359***	**-0.595****	0.067 ^{NS}	**0.619** **	0.333 ^{NS}	**0.584****	**-0.412***	**0.430***	0.025 ^{NS}
Mysella bidentata	0.001 ^{NS}	-0.240 ^{NS}	0.198 ^{NS}	0.138 ^{NS}	0.082 ^{NS}	0.182 ^{NS}	-0.037 ^{NS}	0.198 ^{NS}	-0.196 ^{NS}
Papillicardium papillosum	-0.045 ^{NS}	**0.543** **	0.071 ^{NS}	**-0.449****	-0.157 ^{NS}	-0.295 ^{NS}	0.164 ^{NS}	-0.002 ^{NS}	**0.443****
Parvicardium exiguum	**-0.425** *	-0.278 ^{NS}	**0.385***	**0.356***	0.237 ^{NS}	0.1962 ^{NS}	**-0.3754***	0.053 ^{NS}	-0.048^{NS}
Cerastoderma edule	----------	----------	----------	----------	----------	----------	----------	----------	----------
Abra alba	-0.295 ^{NS}	**-0.378***	0.301 ^{NS}	0.153 ^{NS}	0.272 ^{NS}	**0.348***	-0.266 ^{NS}	**0.481****	-0.063 ^{NS}
Venus verrucosa	0.326 ^{NS}	-0.064 ^{NS}	-0.099 ^{NS}	**-0.382***	0.126 ^{NS}	0.199 ^{NS}	0.247 ^{NS}	0.152 ^{NS}	-0.038 ^{NS}
Dosinia exoleta	0.009 ^{NS}	**0.486****	0.126 ^{NS}	**-0.497****	-0.078 ^{NS}	-0.296 ^{NS}	**0.392***	-0.329 ^{NS}	-0.116 ^{NS}
Venerupis senegalensis	0.004 ^{NS}	0.102 ^{NS}	0.261 ^{NS}	-0.311 ^{NS}	-0.192 ^{NS}	0.053 ^{NS}	0.152 ^{NS}	-0.123 ^{NS}	-0.059 ^{NS}
Hiatella arctica	**0.382***	-0.034 ^{NS}	-0.102 ^{NS}	-0.195 ^{NS}	0.092 ^{NS}	0.160 ^{NS}	0.125 ^{NS}	0.073 ^{NS}	**0.471****
INTERTIDAL									
Species	**G**	**CS**	**MS**	**FS**	**SC**	**OM**	**CA**	**S_o**	**D/H**
Mytilus edulis	**0.333***	**0.347***	-0.069 ^{NS}	**-0.431****	-0.128 ^{NS}	-0.086 ^{NS}	**0.397***	0.288 ^{NS}	-0.058 ^{NS}
Thyasira flexuosa	-0.132 ^{NS}	0.215 ^{NS}	0.173 ^{NS}	-0.104 ^{NS}	0.069 ^{NS}	-0.222 ^{NS}	0.048 ^{NS}	-0.008 ^{NS}	0.271 ^{NS}
Mysella bidentata	**0.321***	**0.468****	0.060 ^{NS}	**-0.357***	-0.117 ^{NS}	-0.284 ^{NS}	**0.388***	0.233 ^{NS}	-0.211 ^{NS}
Papillicardium papillosum	0.245 ^{NS}	0.086 ^{NS}	-0.020 ^{NS}	-0.174 ^{NS}	-0.087 ^{NS}	-0.158 ^{NS}	-0.083 ^{NS}	0.035 ^{NS}	-0.048 ^{NS}
Parvicardium exiguum	0.052 ^{NS}	0.136 ^{NS}	0.043 ^{NS}	0.000 ^{NS}	0.072 ^{NS}	-0.008 ^{NS}	0.119 ^{NS}	0.053 ^{NS}	**-0.373** *
Cerastoderma edule	0.008 ^{NS}	0.094 ^{NS}	0.201 ^{NS}	-0.085 ^{NS}	-0.062 ^{NS}	-0.220 ^{NS}	-0.044 ^{NS}	0.250 ^{NS}	**-0.369** *
Abra alba	0.003 ^{NS}	-0.031 ^{NS}	-0.214 ^{NS}	0.082 ^{NS}	**0.324***	0.185 ^{NS}	0.012 ^{NS}	-0.024 ^{NS}	-0.237 ^{NS}
Venus verrucosa	0.150 ^{NS}	**0.367***	0.023 ^{NS}	-0.178 ^{NS}	0.161 ^{NS}	-0.145 ^{NS}	0.259 ^{NS}	**0.344***	-0.078 ^{NS}
Dosinia exoleta	-0.193 ^{NS}	0.078 ^{NS}	0.201 ^{NS}	-0.119 ^{NS}	-0.037 ^{NS}	-0.119 ^{NS}	0.066 ^{NS}	0.014 ^{NS}	-0.152 ^{NS}
Venerupis senegalensis	0.244 ^{NS}	0.197 ^{NS}	0.011 ^{NS}	-0.205 ^{NS}	0.161 ^{NS}	-0.009 ^{NS}	0.304 ^{NS}	0.228 ^{NS}	**-0.577****
Hiatella arctica	**0.352***	**0.518****	-0.214 ^{NS}	**-0.397***	-0.054 ^{NS}	**-0.319***	**0.446****	0.130 ^{NS}	-0.192 ^{NS}

Table 2. Coefficients of rank correlation (T_s) between densities of the different species (number of individuals in the sample) and physicochemical factors (G : gravel content; CS : coarse sand content, MS medium sand content, FS: fine sand content, SC silt-clay content, OM organic matter content; CA . carbonate content, S_o sorting coefficient; D/H : depth/height with respect to tidal zero). NS : Not significant ($p > 0,05$), *: $p < 0,05$, **: $p < 0,01$

Fig. 3. Estimated densities (individuals per m^2) of *Parvicardium exiguum* (A), *Cerastoderma edule* (B), *Abra alba* (C) and *Venus verrucosa* (D) at sites at which that species was found.

between 0.10 m and 0.94 m. *Mytilus edulis* was found in coarse sands and gravels, at densities of up to 100 individuals/m^2

Generally speaking, the factors most strongly influencing bivalve distribution were grain size and depth, though carbonate content was also an important factor (possibly related to the positive correlation observed between carbonate contents and particle size; $T_s = 0.478$, $p < 0.01$). Anyway *M. bidentata*, *C. edule* and *V. senegalensis* seemed to be less specific in their choice of sediment types.

Species	RA %	Species	RA %
Nucula nitida Sowerby, 1833	0.20	*Parvicardium nodosum* (Turton, 1822)	0.73
Arca tetragona Poli, 1795	0.04	*Cerastoderma edule* (Linnaeus, 1758)	**2.68**
Striarca lactea (Linnaeus, 1758)	0.03	*Spisula elliptica* (Brown, 1827)	0.01
Mytilus edulis galloprovincialis Lamarck, 1818	**19.50**	*Lutraria lutraria* (Linnaeus, 1758)	0.03
Musculus subpictus (Cantraine, 1835)	1.22	*Phaxas pellucidus* (Pennant, 1977)	0.01
Pecten maximus (Linnaeus, 1758)	0.33	*Moerella donacina* (Linnaeus, 1758)	0.37
Anomia ephippium Linnaeus, 1758	1.4	*Moerella pusilla* (Philippi, 1836)	0.01
Pododesmus squamula (Linnaeus, 1758)	1.5	*Gobraeus tellinella* (Lamarck, 1818)	1.02
Monia patelliformis (Linnaeus, 1767)	0.1	*Gobraeus depressa* (Pennant, 1777)	1.01
Ostrea edulis Linnaeus, 1758	0.41	*Scrobicularia plana* (da Costa, 1778)	0.04
Crassostrea gigas (Thunberg, 1793)	0.01	*Abra nitida* (O.F.Müller, 1776)	0.22
Pisidium casertanum (Poli, 1791)	0.01	*Abra alba* (Wood, 1802)	**2.27**
Loripes lacteus (Linnaeus, 1758)	0.18	*Venus verrucosa* Linnaeus, 1758	**1.73**
Lucinoma borealis (Linnaeus, 1767)	0.13	*Gouldia minima* (Montagu, 1803)	0.81
Myrtea spinifera (Montagu, 1803)	1.02	*Dosinia exoleta* (Linnaeus, 1758)	**2.06**
Lucinella divaricata (Linnaeus, 1758)	0.02	*Tapes decussatus* (Linnaeus, 1758)	0.03
Thyasira flexuosa (Montagu, 1803)	**3.9**	*Venerupis rhomboides* (Pennant, 1777)	1.12
Lasaea rubra (Montagu, 1803)	0.04	*Venerupis saxatilis* (Fleuriau de Bellevue, 1802)	1.01
Kellia suborbicularis (Montagu, 1803)	1.21	*Venerupis senegalensis* (Gmelin, 1791)	**5.63**
Montacuta substriata (Montagu, 1808)	0.01	*Chamelea striatula* (da Costa, 1778)	0.44
Mysella bidentata (Montagu, 1803)	**35.62**	*Clausinella fasciata* (da Costa, 1778)	0.75
Digitaria digitaria (Linnaeus, 1758)	0.19	*Timoclea ovata* (Pennant, 1777)	0.04
Goodallia triangularis (Montagu, 1803)	0.03	*Corbula gibba* (Olivi, 1792)	1.02
Acanthocardia paucicostata (Sowerby, 1841)	0.01	*Hiatella arctica* (Linnaeus, 1767)	**1.80**
Papillicardium papillosum (Poli, 1795)	**4.59**	*Nototeredo norvegica* (Splenger, 1792)	0.11
Parvicardium exiguum (Gmelin, 1791)	**2.53**	*Thracia papyracea* (Poli, 1791)	1.11

Table 3. List of the species detected in the present study showing overall relative abundance (i.e. percentage of the total number of individuals found in all samples).

DISCUSSION

Interpretation of spatial variations in the abundance of benthic species is difficult, in view of the large number of environmental factors which may act on benthic communities. PEARSON & ROSENBERG (1978) studied the factors involved in structuring the marine benthos, and highlighted the importance of food availability as a determinant of community structure. They concluded that depth, latitude and water current speed are the factors which have the strongest effect on food availability. PETERSON (1979) reported that the factors affecting abundance in the benthos may be divided into density-dependent factors (such as competition, predation, and adult-larva interactions) and the physical properties of the sediment.

In our study area, the most important environmental factors affecting the distribution of bivalves were particle size and depth/ height. The current regime was not investigated, though it is clearly determinant of the distribution of sediment types.

The dominant species in the intertidal area, *Mytilus edulis, Parvicardium exiguum* and *Cerastoderma edule*, showed a relationship with physicochemical factors that was consistent with their autoecology. *M. edulis*, which feeds on suspended detritus and phytoplankton, is found primarily on coarse sediments that allow it to attach itself by its byssus (TEBBLE, 1966). In the present study, the density of this species correlated positively with coarse sediment content and negatively with fine sand content. Both *P. exiguum* and

Fig. 4. Estimated densities (individuals per m^2) of *Dosinia exoleta* (A), *Venerupis senegalensis* (B), and *Hiatella arctica* (C) at sites at which that species was found.

C. edule are highly tolerant of variations in salinity, and are typically indifferent to the type of substrate (TEBBLE, 1966); the most important factors governing their distribution are the emersion time and water current speed, both related to food availability (FIGUERAS, 1956), since they are filter-feeders that can only feed when submerged (LABORDA, 1986). In the present study we found that the densities of both species in the intertidal zone were negatively correlated with height with respect to tidal level zero, while there were no significant correlations with the other environmental parameters. *Venerupis senegalensis* was also abundant in the intertidal domain, with the most important factor in its distribution being height: like most venerids, it is adapted to the lower levels of the intertidal zone or to the subtidal zone. The importance of tidal level and zoning has been discussed at length by other authors (WOLFF, 1973; RAFAELLI & BOYLE, 1986; JUNOY & VIÉITEZ, 1990). The distribution of this species did not show any clear relationship with sediment characteristics, in accordance with previous reports: TEBBLE (1966), for example, found that this species that inhabits all kinds of bottoms (sand, sandy gravel, silty gravel, and silty sand), while in Kilkieran Bay in Ireland, KEEGAN (1974) reported the presence of this species in a great variety of biotopes, including bottoms with clean sand, silty sand, maërl and on rare occasions even conchiferous gravel. However, a study by MORA (1980) in the Ria de Arousa (in southern Galicia), found this species to be limited to clean sand and gravel.

Of the dominant species in the subtidal zone, *Mysella bidentata* had a broad distribution throughout the inlet, with high densities of individuals. The density of this species in the subtidal zone showed no correlation with any of the physicochemical parameters in accordance with the fact that it is a highly ubiquitous species, able to exploit a wide variety of environments, from sandy to those with high contents of fine particles. It is also characterized by its feeding behavior, which changes depending on developmental stage: juveniles are deposit-feeders while adults are filter-feeders (OCKELMANN & MUUS, 1978). *Thyasira flexuosa* showed a strong positive correlation with fine sand and organic matter contents; similarly, other authors such as LÓPEZ-JAMAR *et al.* (1987) have reported that this species inhabits silty sediments with a relatively high organic matter content. This species has morphological adaptations that prevent clogging of the branchial filter by large particles in suspension (ALLEN, 1958). Endosymbiont bacteria, which probably contribute to its diet, are found in the gills (DANDO *et al.*, 1985). In our study area, the density of *Abra alba* correlated positively with the sorting coefficient (which indicates that it appears in poorly sorted sediments, with a wide diversity of particles) and to a lesser extent with organic matter content. GLÉMAREC (1973) reports on the presence of this species in heterogeneous silty facies. According to DAUVIN & GENTIL (1989), it is plentiful in silt and sand sediments, tolerates physicochemical changes in the sediment very well, and is rapidly adaptable (strategist r). LANDE (1975) highlights the presence of this species in heterogeneous sediments, and CORNET (1985) states that it can live on highly varied bottoms, and that substrate granulometry is not a decisive factor, although it requires a layer of suspended detritus in the water-sediment interphase as a source of food (GLÉMAREC, 1964).

Venus verrucosa, Dosinia exoleta and Hiatella arctica are species that live on bottoms characterized by coarse sand, silt gravel or conchiferous gravel (TEBBLE, 1966). In our study area, they occurred largely on coarse sand and gravel, and the densities of these species were negatively correlated with fine sand content.

The observed correlations between the densities of the different species and particle size and organic matter content appear to be related to feeding behaviour. For example, the densities of *T. flexuosa* and *A. alba*, which are burrowing detritus feeders, correlated positively with organic matter and fine sand contents, whereas the remaining species (with the exception of *M. bidentata* which may change its feeding mechanism depending on its developmental stage) fed on particles in suspension, so that their distribution correlates positively with sediments having a larger particle size. According to CORNET (1986), filter-feeders take over from detritus-feeders species when the proportion of fine particles decreases. LEVINTON (1977) reports that deposit-feeders dominate in ecosystems with fine, soft sediments and that their presence is linked to the silt-clay fraction, although this latter has not been verified in our study area. By contrast, filter-feeders dominate in sandy sediments (SANDERS, 1958) and their distribution may be governed more by hydrodynamic processes, which determine sediment characteristics, than by the characteristics of the sediment itself.

The marked overlap in the distribution of *A. alba* and *T. flexuosa* is as expected given that these species characteristically form part of a well-defined subtidal zone community (see THORSON, 1957). *Mysella bidentata*, which likewise showed considerable overlap with these two species, is not characteristic of this community but is ubiquitous and broadly distributed in our study area. *Hiatella arctica, V. verrucosa* and *V. senegalensis*, similarly showed overlapping distributions, and all three occurred at high densities on a maërl bed near Punta Redonda. This bed is made up of *Lithothamniom corallioides* and *Phymatolithon calcareum*, on a shell-gravel bottom with a small amount of silt. According to URGORRI *et al.* (1992), these bottoms offer stable substrates which provide good shelter for many species of small molluscs including the juveniles of certain species, so that the maërl acts as a hatchery.

The similar distributions in some areas of *P. exiguum* and *V. senegalensis* may be explained by the fact that these species are characteristic of the intertidal facies occupied by *Zostera noltii* within the limited community of *Macoma balthica* (THORSON, 1957).

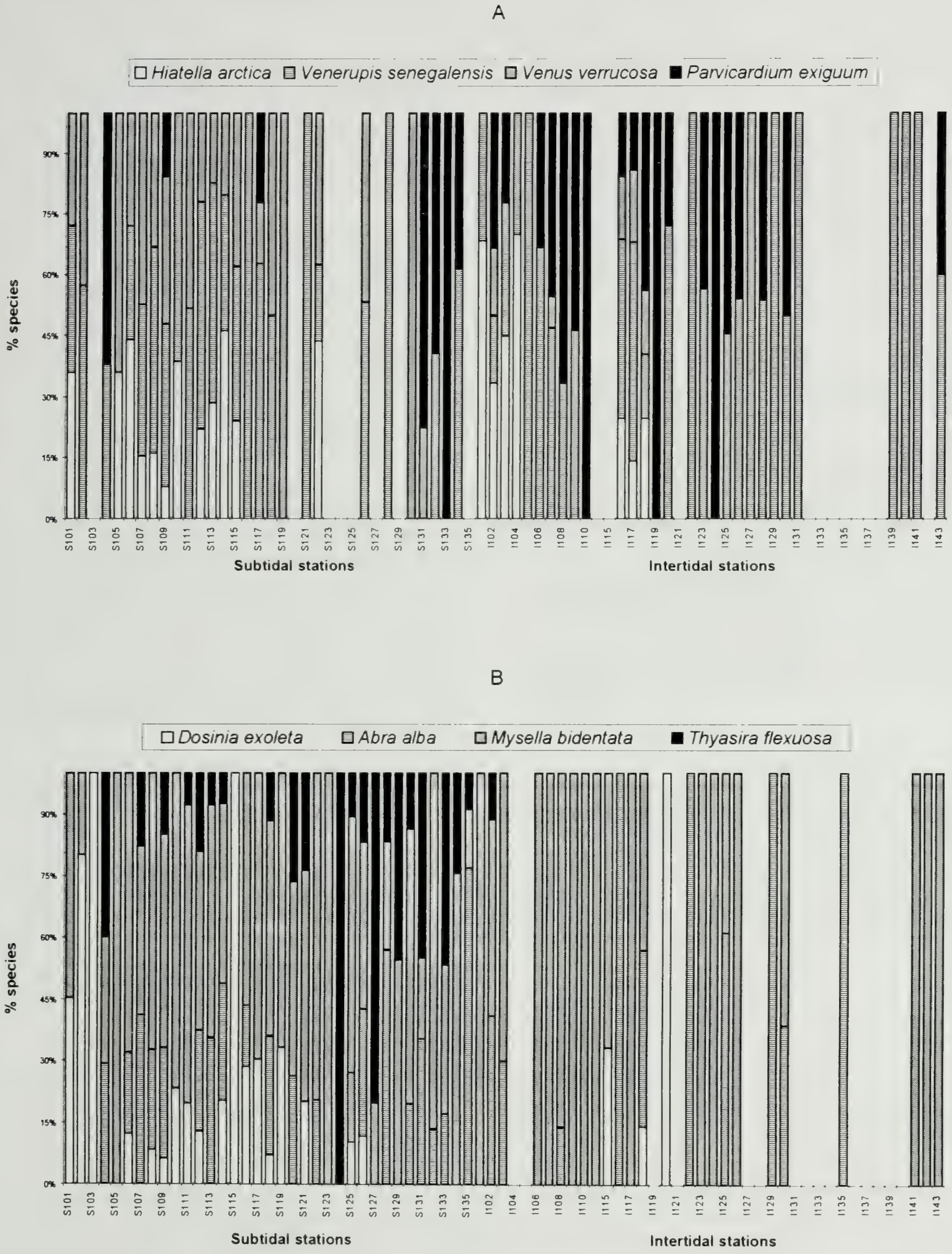

Fig. 5. Plots illustrating the overlaps in the distributions of *Hiatella arctica*, *Venus verrucosa*, *Venerupis senegalensis* and *Parvicardium exiguum* (A) and *Abra alba*, *Mysella bidentata*, *Thyasira flexuosa* and *Dosinia exoleta* (B). The horizontal axis shows sample number. The vertical axis shows relative abundance, here defined as the number of individuals in that sample expressed as a percentage of the maximum number of individuals per sample recorded for that species

This has likewise been reported by CURRÁS & MORA (1991) in the Ría de Ribadeo (likewise on the north coast of northwest Spain), where *P. exiguum and V. senegalensis* were found on muddy sand or sandy mud bottoms covered by *Z. noltii*. This phanerogam gives rise to a more diversified habitat, and its rhizomes and roots compact the sediment and provide protection from predators (ECKMAN, 1987). Both population densities and species richness are thus typically higher.

Finally, *H. arctica* and *V. verrucosa* showed closely overlapping distributions since both occurred in the dumping area of the dredging operations carried out in the channel of the ría. The dumped material is characterized by coarse gravel and conchiferous gravel, which are typical habitats for these species.

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Description of eight new species of Muricidae (Gastropoda)

Roland HOUART

Research associate, Institut royal des Sciences naturelles de Belgique
Département des Invertébrés Récents
Rue Vautier, 29, B-1000 Brussels, Belgium

KEYWORDS. Gastropoda, Muricidae, new species.

ABSTRACT. The following new species of Muricidae are described, and compared with related species: *Attiliosa edingeri* and *Favartia eastorum* from Western Australia, *Favartia deynzeri* from the Red Sea, *Apixystus rippingalei* from Queensland, *Trophonopsis bassetti* from New South Wales and Queensland, *Orania rosadoi* from Mozambique, *Ergalatax dattilioi* from the Philippine Islands, Indonesia, and Japan, and *Thais herberti* from South Africa.

RESUME. Les espèces suivantes sont décrites et comparées avec des espèces apparentées: *Attiliosa edingeri* et *Favartia eastorum* d'Australie Occidentale, *Favartia deynzeri* de la Mer Rouge, *Apixystus rippingalei* du Queensland, *Trophonopsis bassetti* de la Nouvelle-Galles du Sud et du Queensland, *Orania rosadoi* de Mozambique, *Ergalatax dattilioi* des Philippines, d'Indonésie et du Japon, et *Thais herberti* d'Afrique du Sud.

INTRODUCTION

New species of Muricidae continue to be discovered thanks to dredging programs, expeditions, and private collecting. The eight new species described here originate from different sources: *Attiliosa edingeri*, *Favartia eastorum*, *F. deynzeri* and *Orania rosadoi* were recently discovered by private collectors; *Apixystus rippingalei* and *Trophonopsis bassetti* were collected during several cruises by HMAS *Kimbla* (1976, 1977, 1984), and FRV *Kapala* (1975, 1977, 1979) (material housed in Australian Museum, Sydney); *Ergalatax dattilioi* by private collectors, and during the MUSORSTOM 1 expedition (1976), by R.V. *Vauban* off the Philippine Islands, and the KARUBAR expedition (1991), by R.V. *Baruna Jaya I* in the Banda and Arafura Seas, and off the Kai and Tanimbar Islands, Eastern Indonesia (material housed in Muséum National d'Histoire Naturelle, Paris); *Thais herberti* during the Natal Museum Dredging Program, 1989 (Natal Museum, Pietermaritzburg).

Abbreviations

AMS: The Australian Museum, Sydney, Australia.
BMNH: The Natural History Museum, London, Great Britain.
IRSNB: Institut royal des Sciences naturelles de Belgique.
MNHN: Muséum National d'Histoire Naturelle, Paris, France.
NM: Natal Museum, Pietermaritzburg, South Africa.
NMNZ: Museum of New Zealand, Wellington.
QM: Queensland Museum, Brisbane, Australia.
WAM: Western Australian Museum, Perth, Australia.

dd: empty shell.
lv.: live-taken specimen.

SYSTEMATIC ACCOUNT

Family **MURICIDAE** Rafinesque, 1815
Subfamily **MURICINAE** Rafinesque, 1815
Genus ***Attiliosa*** Emerson, 1968

Type species (by original designation): *Coralliophila incompta* Berry, 1960 (= *Peristernia nodulosa* A. Adams, 1854); Recent, Eastern Pacific.

Remarks.

When I described *Attiliosa goreensis* (HOUART, 1993) from Senegal, I recorded that four species and one subspecies of *Attiliosa* were known at that time: *A. nodulosa* (A. Adams, 1855) from the Eastern Pacific; *A. nodulifera* (Sowerby, 1841), and its subspecies *caledonica* Jousseaume, 1881 from the Indo-West Pacific; *A. philippiana* (Dall, 1889) from Florida, and *A. aldridgei*, known from different localities in the Western Atlantic. Since then, in addition to *A. goreensis*, other species of *Attiliosa* have been described: *A. bozzettii* Houart, 1993 from Somalia, *A. glenduffyi* Petuch, 1993 from the Dominican Republic, and *A. ruthae* Houart, 1996 from the Philippine Islands. Moreover, in 1993 I neglected to mention *A. orri* (Cernohorsky, 1976) from the Andaman Islands.

Since the description of *A. goreensis*, I have had the opportunity to examine additional specimens of *A. nodulifera caledonica*, including a specimen from Mindanao, Philippine Islands (Fig. 31). The shell is large, almost 28 mm in length and dark brown while other specimens of *A. caledonica* are usually white. However, apart from colour, and size, I cannot separate it from typical specimens of *A. caledonica*. Since *A. nodulifera* lives throughout the Philippine Islands, it seems now that *A. caledonica* should be raised to specific rank. However, *A. nodulifera* is not yet recorded from other localities where *A. caledonica* occurs, such as New Caledonia and Polynesia (TRÖNDLE & HOUART, 1992).

Attiliosa edingeri n.sp.

Figs 1-4, 40

Type material examined.

Western Australia: off Esperance, 34-36 m, holotype WAM S.1101 and 1 paratype WAM S.1102; off Esperance, amongst weed, sand and rubble, 31 m, 1 paratype coll. A. Edinger; 1 paratype coll. R. Houart (all lv.).

Distribution.

Off Esperance, Western Australia, taken alive at 31-36 m.

Description.

Shell biconical, large for the genus, up to 35.7 mm in length at maturity; lightly built, squamous. Spire high, with 1.5 protoconch whorls and up to 6 broad, convex, weakly shouldered teleoconch whorls. Suture adpressed. Protoconch small; whorls rounded, smooth; terminal varix unknown (eroded). Axial sculpture of teleoconch whorls consisting of low, rounded, squamous ribs and of numerous growth lamellae. First whorl with 11 ribs, second to fifth with 11 or 12 ribs, last whorl with 9 ribs. Spiral sculpture of weak, squamous, rounded, primary and secondary cords and some weak, squamous threads. First whorl with 2 cords and 2 or 3 threads on shoulder, second to fourth with 2 or 3 cords and 3 or 4 threads on shoulder, penultimate with 3 or 4 cords and 3-6 threads on shoulder, last adult whorl with 12-16 cords and 4-6 shallow, squamous threads on shoulder.

Aperture large, ovate; columellar lip smooth; lip weakly erect partially, adherent at adapical extremity; anal notch shallow, broad; outer lip crenulate, with 7 weak, elongate denticles within; denticles occasionally absent. Siphonal canal short, broad, strongly abaperturally recurved at extremity, with 2 or 3 squamous spiral cords and single thread.

Light tan or orange with darker coloured spiral band on periphery of last whorl, occasionally lighter coloured axial ribs. Aperture white.

Operculum dark brown, ovate, with terminal nucleus.

Radula with a long, broad central cusp; narrow, long, lateral cusps with broad base. Lateral teeth sickle shaped, broad.

Remarks.

Attiliosa edingeri n.sp. is highly distinctive from any known Indo-Pacific species of *Attiliosa*. It differs from *A. nodulifera, A. caledonica, A. ruthae* and *A. orri* in having a spineless shell, and from these species and *A. bozzettii*, in having more conspicuous, numerous, and squamous spiral cords and threads, a smooth columellar lip, and a broader aperture relative to the shell length. It is currently the largest known Recent species of *Attiliosa*.

Etymology.

Named for Andrew Edinger, Mandurah, Western Australia, who, together with Peter Clarckson, discovered the habitat of the new species, and sent it to me for identification.

Subfamily **MURICOPSINAE**

Radwin & D'Attilio, 1971

Genus ***Favartia*** Jousseaume, 1880

Type species (by original designation): *Murex breviculus* Sowerby, 1834; Recent, Indo-West Pacific.

Favartia eastorum n.sp.

Figs 5-7

Type material examined.

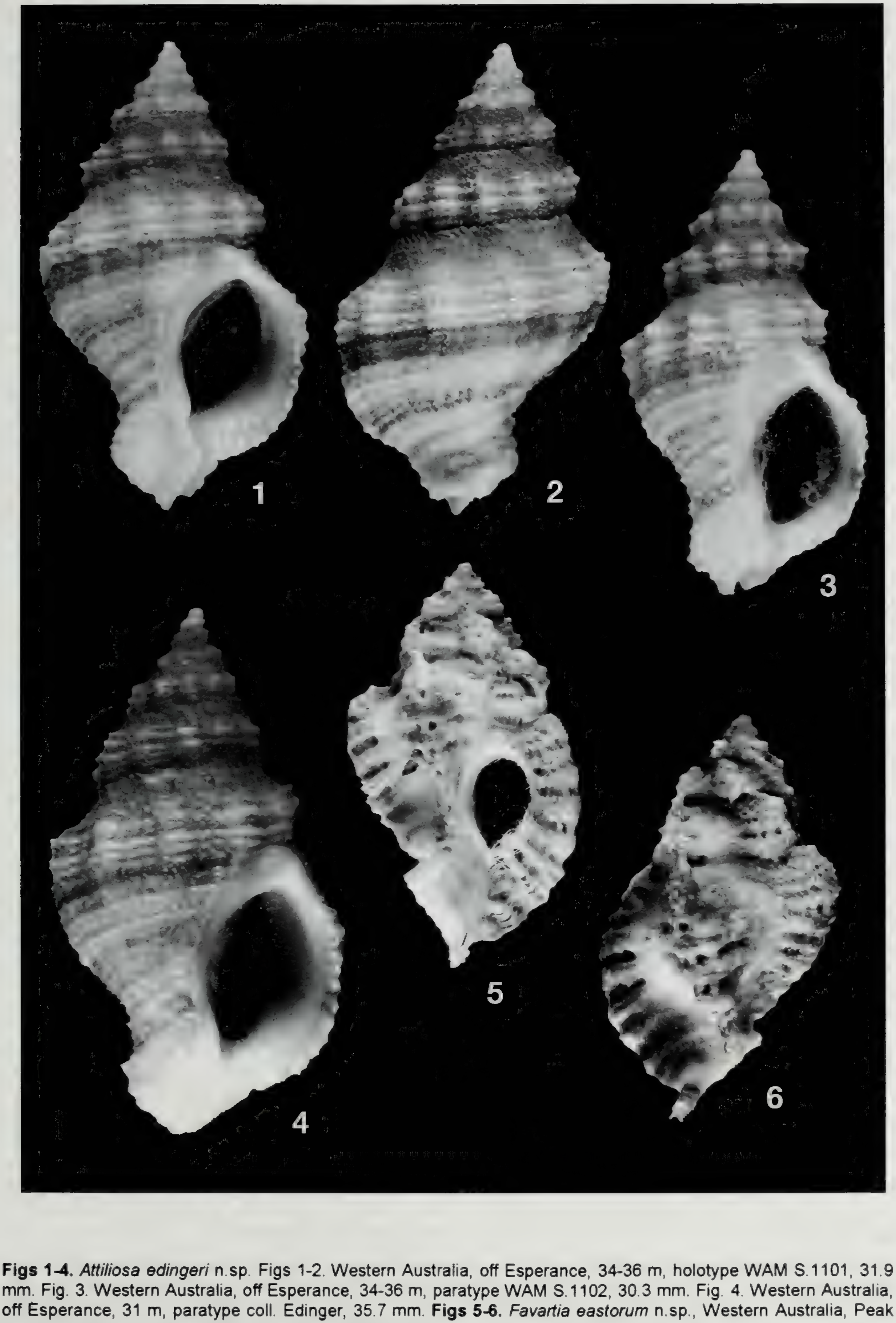
Western Australia: Peak Island, N of Exmouth Gulf, WA; 21°36' S, 114°36' E, 24-27 m, buried in silty sand pockets, shelving limestone reef with sparse covering of small sponges, gorgonians, and hard corals, holotype WAM S.1103; paratypes 1 WAM S.1104; 1 AMS C. 203326; 1 coll. R. Houart (all lv.).

Distribution.

Peak Island, N of Exmouth, Western Australia, taken alive at 24-27 m.

Description.

Shell of medium size for the genus, up to 21.5 mm in length at maturity, tuberculate. Spire high, up to 5 weakly convex, shouldered teleoconch whorls, suture



Figs 1-4. *Attiliosa edingeri* n.sp. Figs 1-2. Western Australia, off Esperance, 34-36 m, holotype WAM S.1101, 31.9 mm. Fig. 3. Western Australia, off Esperance, 34-36 m, paratype WAM S.1102, 30.3 mm. Fig. 4. Western Australia, off Esperance, 31 m, paratype coll. Edinger, 35.7 mm. **Figs 5-6.** *Favartia eastorum* n.sp., Western Australia, Peak Island, N of Exmouth Gulf, WA, 21°36' S, 114°36' E, 24-27 m, holotype WAM S.1103, 21.4 mm.

adpressed. Protoconch unknown (eroded). Axial sculpture of teleoconch whorls consisting of high, strong, broad, rounded varices: first and second whorls with 5 or 6 varices, third and fourth with 4 or 5, last whorl with 4 varices. Spiral sculpture of high, strong, nodose primary cords; secondary cords on shoulder and siphonal canal: spiral sculpture of first whorl eroded, second with 2 cords on whorl, 2 on shoulder; third with one on whorl, 2 or 3 on shoulder, fourth with 2 on whorl, 2 on shoulder, last whorl with 5 on whorl and 3 on shoulder; cords more strongly developed on axial varices, shallow or/and eroded on early whorls.

Aperture small, ovate; columellar lip flaring, narrow, smooth, rim partially erect, adherent at adapical extremity; anal notch shallow, broad; outer lip erect, crenulate, smooth within. Siphonal canal short, broad, abaperturally recurved at extremity, narrowly open, with 2 or 3 smooth, or almost obsolete spiral cords.

Light tan with darker coloured blotches, mostly on spiral cords. Aperture white.

Operculum dark brown, ovate-elongate with terminal nucleus. Radula unknown.

Remarks.

Favartia confusa Brazier, 1877 (Figs 8-9) differs in having a larger shell relative to the number of teleoconch whorls. Furthermore, in *F. confusa* the siphonal canal is markedly straighter, the spiral cords are narrower, the varices are broader and flanged adapically and abapically; abapical flange almost smooth, extending up to the extremity of the siphonal canal.

Favartia cyclostoma (Sowerby, 1841) has a broader, more shouldered shell with more numerous, narrower spiral cords, more fimbriated varices, and a more rounded aperture.

Etymology.

At the request of Peter Clarckson, the species is named for Milton and Aileen East, of Geraldton, West Australia, who first showed him a specimen from their collection.

Favartia deynzeri n.sp.

Figs 10-13

Type material examined.

Red Sea: Egypt, Shab Shareer, 15-20 m, holotype IRSNB IG 28515/478. Paratypes: 1 coll. A. Deynzer; 1 coll. R. Houart (all lv.).

Distribution.

Shab Shareer, Egypt, taken alive at 15-20 m.

Description.

Shell medium sized for the genus, up to 17.18 mm in length at maturity (holotype), heavy, moderately spinose. Spire high with 1.5 protoconch whorls and up to 5 broad, angulate, weakly shouldered teleoconch whorls. Suture impressed, partially obscured by small axial lamellae. Protoconch small, globose, whorls rounded; terminal varix unknown (eroded). Axial sculpture of teleoconch whorls consisting of 4 or 5 high, strong, broad, rounded varices from first to last whorl; varices more developed on shoulder. Spiral sculpture of high, strong, squamous cords: two spiral cords on early whorls; last whorl with 5 cords, ending as short spinelike projections on varices; last whorl occasionally with minor spiral threads.

Aperture small, ovate; columellar lip narrow, flaring, smooth, rim partially erect, adherent at adapical extremity; anal notch obsolete; outer lip erect, crenulate, with 4 or 5 weak, occasionally obsolete, lirae within. Siphonal canal moderately long, broad, straight, abaperturally recurved at extremity, narrowly open, with 3 or 4 frondose, short spinelets.

Creamy-white, occasionally with light tan blotches on spiral cords or shoulder; aperture white.

Operculum dark brown, ovate, with terminal nucleus. Radula unknown.

Remarks.

Favartia deynzeri is highly distinctive from any other Indo-West Pacific or Red Sea species of *Favartia* by its form, sculpture and particular ornamentation of the siphonal canal. *F. cyclostoma* (Sowerby, 1841) and *F. sykesi* (Preston, 1904) which superficially resemble *F. deynzeri*, have a larger and broader shell, with more numerous, narrower varices, and narrower, larger siphonal canal with different ornamentation.

Etymology.

Named for Al Deynzer, Sanibel, Florida, who sent me the shells for identification.

Subfamily **TROPHONINAE** (*sensu lato*) Cossmann, 1903

Genus *Apixystus* Iredale, 1929

Type species (by original designation): *Trophon stimuleus* Hedley, 1907; Recent, North-East Australia.

Apixystus rippingalei n.sp.

Figs 14-16, 46

Type material examined.

Queensland: E. of Lady Musgrave Island, 23°52.5' -

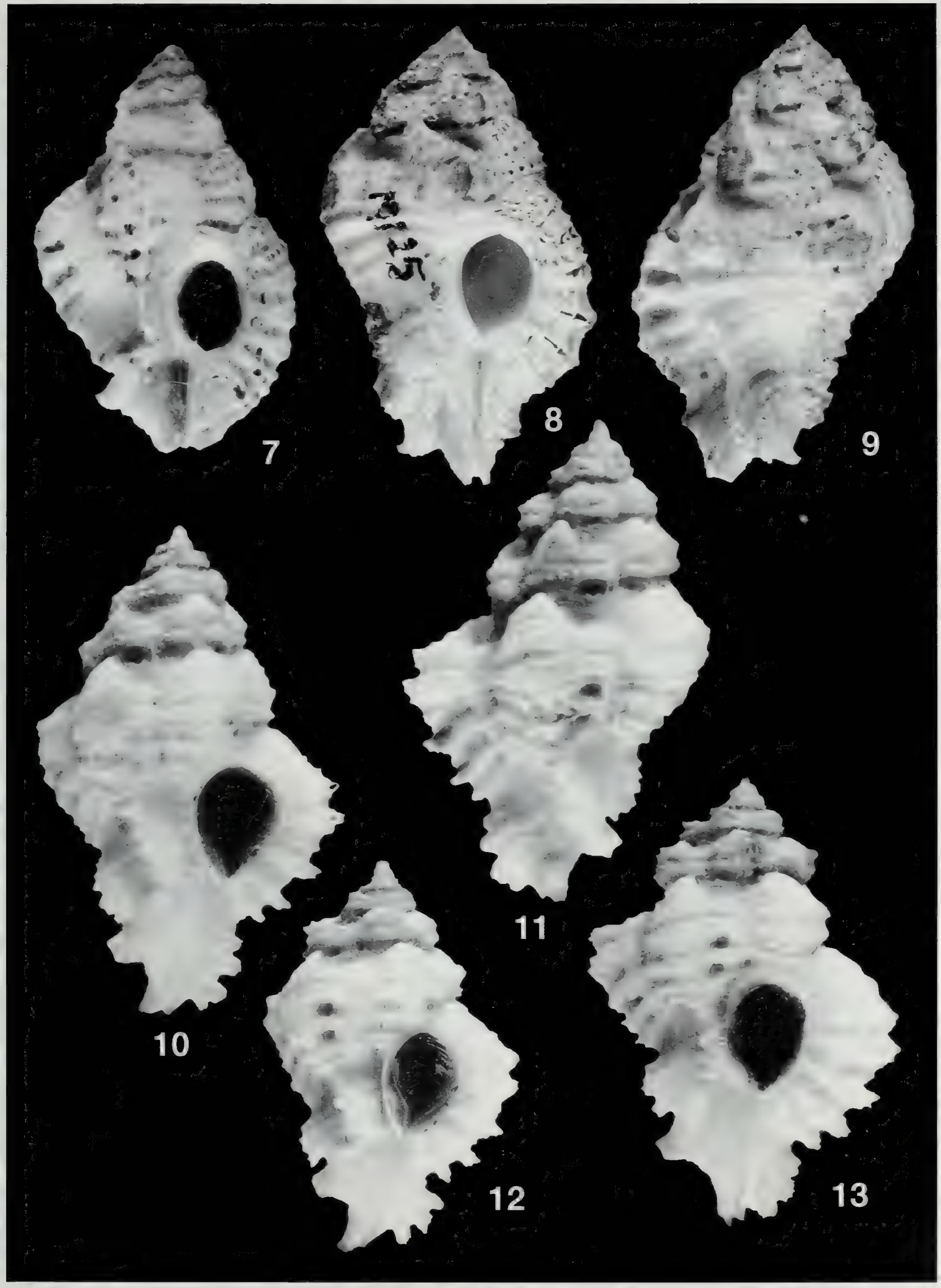


Fig. 7. *Favartia eastorum* n.sp. Western Australia, Peak Island, N of Exmouth Gulf, WA, 21°36' S, 114°36' E, 24-27 m, paratype coll. R. Houart, 18.8 mm. **Figs 8-9.** *Favartia confusa* (Brazier, 1877). Australia, Queensland, Darnley Id, Torres Strait, 55 m, holotype AMS C.077183, 26.8 mm. **Figs 10-13.** *Favartia deynzeri* n.sp. Red Sea, Egypt, Shab Shareer, 15-20 m. **Figs** 10-11. Holotype IRSNB IG 28515/478, 17.2 mm. Fig. 12. Paratype coll. R. Houart, 13 mm. Fig. 13. Paratype coll. A. Deynzer, 15.6 mm.

23°51.9' S, 152°42.7' - 152°41.7' E, 296 m, holotype AMS C.313232 (dd)

Paratypes: 42 AMS C.313230, 1 BMNH 1996286, 1 MNHN, 1 NM L4346/T1519, 1 NMNZ M.272617, 1 QM MO. 61758, 2 coll. R. Houart (all dd).

Other material examined.

Queensland: SE of Swain Reefs, 22°26.27' - 22°20.2' S, 153°17.13' - 152°17.6' E, 187 m, AMS C.321907 (37); Capricorn Channel, 23°8.6' S, 152°16.6' E, 155 m, AMS C.321954 (1); E of North West Is, Capricorn Channel, 23°15.2' S, 152°24.1' E, 284 m, AMS C.321963 (1); 24.5 ml E of Lady Musgrave Island, 23°33.7' S, 152°37' E, 339-348 m, AMS C.125294 (3); of Sandy Cape, 24°43.5' - 24°43.8' S, 153°33.4' - 153°33.3' E, 604 m, AMS C.313229, (1); off Maroochydore, 26°41.2' S, 153°38.4' E, 200 m, AMS C.321943, (1); off Cape Moreton, 27°0' S, 153°34' - 153°36' E, 128-183 m, AMS C.150076, (3) (all dd).

Distribution.

Queensland, Australia, in 128-604 m (Fig. 46).

Description.

Shell medium sized for the genus, up to 4.4 mm in length, spinose, delicate. Spire high with 1.5-1.75 protoconch whorls and up to 4 angulate, shouldered, spinose, teleoconch whorls. Suture impressed. Protoconch large, globose, whorls rounded, smooth; terminal varix shallow, delicate, thin, weakly curved. Axial sculpture of teleoconch whorls consisting of narrow, spinose lamellae: first whorl with 7 or 8 lamellae, second with 10 or 11, third with 12-14, last whorl with 14 lamellae. Spiral sculpture of low, weak, smooth cords on first teleoconch whorl, and of high, rounded cords on other whorls, ending as short spines; shoulder spines more conspicuous. First and second whorl with 2 or 3 cords, third with 3 or 4 cords, last whorl with 4 cords.

Aperture moderately small, rounded; columellar lip flaring, smooth, rim partially erect, adherent at adapical extremity; anal notch obsolete; outer lip undulate, with 4 weak or strong, elongate denticles within. Siphonal canal moderately long, 16-23 % of total shell length; open, smooth or occasionally with a single, smooth, medial spiral cord.

Transluscent white.

Radula and operculum unknown.

Remarks.

The shell sculpture in species of *Apixystus* is interspecifically and intraspecifically rather uniform. *Apixystus stimuleus* (Hedley, 1907) (Fig. 17) has 9 or 10, less frilly axial lamellae on the last teleoconch whorl, the shoulder spines are broader and shorter; there are 2 spiral cords on the penultimate whorl instead of 3, and 2 or 3 low spiral cords on the last whorl, instead of the 4 strong, high cords. *A. leptos* Houart, 1995 (Figs 18-19) has 2 spiral cords on the penultimate whorl, 2 on the last whorl, occasionally with 2 low, shallow threads abapically; the spines are shorter, and the siphonal canal is shorter and more weakly recurved. *A. recurvatus* (Verco, 1909) (Figs 20-21) is relatively larger, less shouldered, with fewer, lower axial lamellae, shorter spines, and lower spiral sculpture.

Etymology.

Named in memory of the late Oswald (Ossie) H. Rippingale, Margate Beach, Queensland, friend, artist and shell lover.

Genus *Trophonopsis* Bucquoy & Dautzenberg, 1882

Type species (by original designation): *Murex muricatus* Montagu, 1803, Recent, Mediterranean, North-East Atlantic.

Trophonopsis bassetti n.sp.

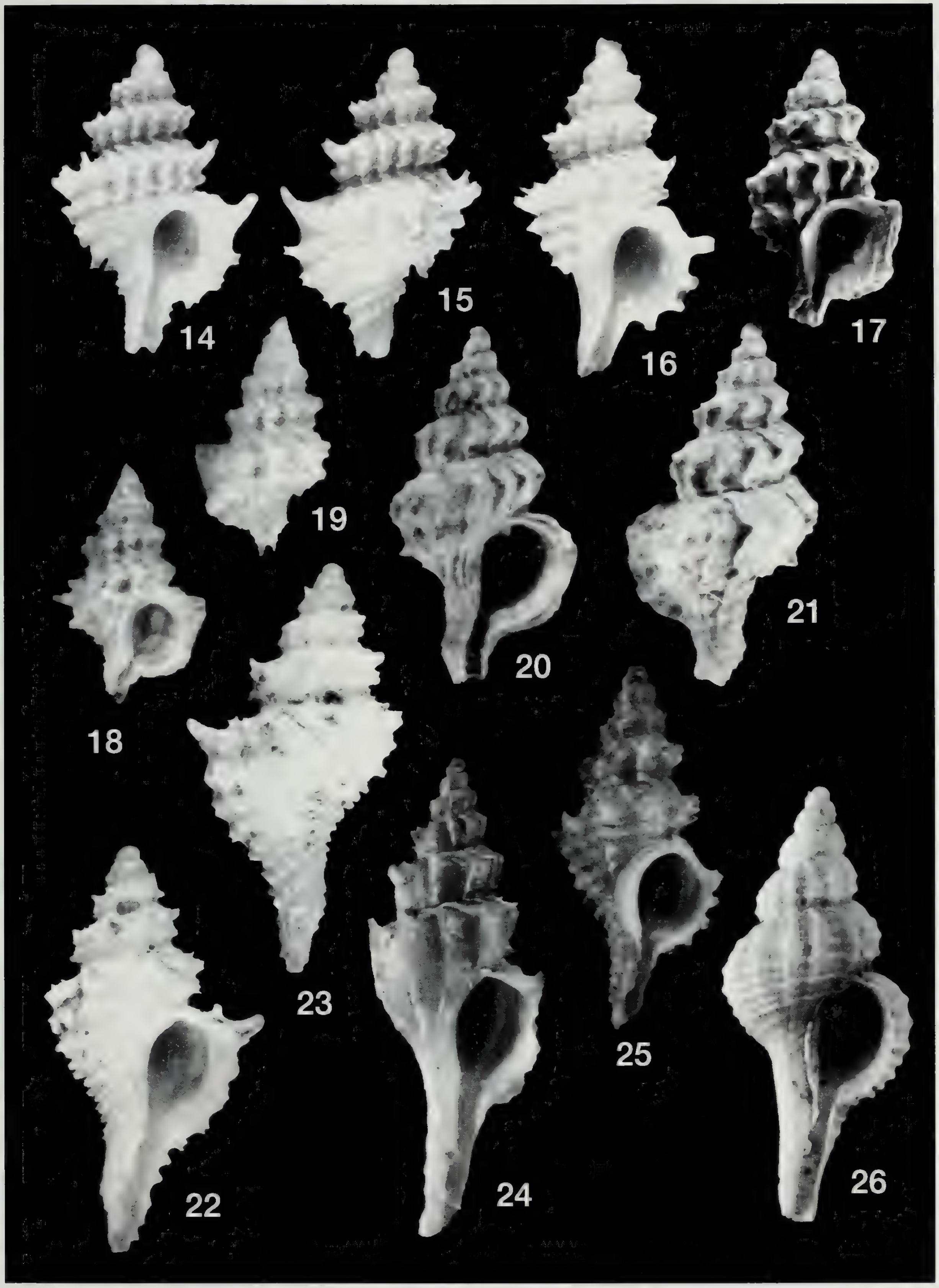
Figs 22-23, 47

Type material.

New South Wales: SE of Clarence River, 29°41' - 29°32' S, 153°45 - 153°47' E, 405-412 m, holotype AMS C.313223 (lv.), and 1 paratype coll. R. Houart (dd).

Other paratypes: Queensland: E of Lady Musgrave Island, 23°52.5' - 23°51.9' S, 152°42.7 - 152°41.7' E, 296 m, 1 AMS C.313231 (lv.); New South Wales: E of Cape Three Points, 33°28' - 33°29' S, 152°4' - 152°3' E, 457-476 m, 2 AMS C.321596 (dd); off Sydney, 34°4.2' S, 151°37.4' E, 393 m, 1 AMS C.322783 (lv.); off Ulladulla, 35°30' - 35°33' S, 150°48' - 150°47' E, 549 m, 1 AMS C.313224 (dd).

Figs 14-16. *Apixystus rippingalei* n.sp. Australia, Queensland, off Lady Musgrave Id, 296 m, Figs14-15. Holotype AMS C.313232, 4 mm. Fig. 16. Paratype AMS C.313230, 4.4 mm. **Fig. 17.** *A. stimuleus* (Hedley, 1907). NSW, Sydney, 22 miles east of Narrabeen, 146 m, holotype AMS C.25797, 3.3 mm. **Figs 18-19.** *A. leptos* Houart, 1995. New Caledonia, holotype MNHN, 4.8 mm. **Figs 20-21.** *A. recurvatus* (Verco, 1909). NSW, off Sydney, AMS C.150080, 7 mm. **Figs 22-23.** *Trophonopsis bassetti* n.sp. Australia, NSW, SE of Clarence River, 405-412 m, holotype AMS C.313223, 8.9 mm. **Fig. 24.** *Trophonopsis plicilaminatus* (Verco, 1909). South Australia, off Beachport, 200 fms (365 m), paratype AMS C.31093, 15.9 mm. **Fig. 25.** *Trophonopsis segmentatus* (Verco, 1909). South Australia, off Cape Jaffa, 90 fms (165 m), paratype AMS C.31065, 9.5 mm. **Fig. 26.** *Trophonopsis simplex* (Hedley, 1903). NSW, Sydney, off Port Hacking, coll. R. Houart, 11 mm.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Distribution.

New South Wales and Queensland, Australia, 296-549 m, taken alive in 296-393 m (Fig. 47)

Description.

Shell medium sized for the genus, up to 13.9 mm in length at maturity (paratype AMS C.321596), slender, weakly spinose, delicate. Spire high with 1.5 protoconch whorls and up to 4.5 shouldered, spinose teleoconch whorls. Suture impressed. Protoconch large, globose; whorls rounded, glossy; terminal varix thin, low, weakly curved. Axial sculpture of teleoconch whorls consisting of low, weak lamellae. Lamellae more strongly developed on shoulder, occasionally producing short, spinelike projections: 7 or 8 lamellae on first whorl, 10-12 on second, 11-13 on third, 11-15 on last whorl. Spiral sculpture of broad, rounded cords: first, second and third whorl with 2 cords, last whorl with 5; shoulder smooth, except axial lamellae, occasionally with single, low, shallow cord on last whorl.

Aperture moderately small, angulate; inner lip almost horizontal, forming an angle of approximately 85-86° with axis of shell; columellar lip smooth, adherent; anal notch shallow; outer lip smooth, with 3 weak, low denticles within; adapical denticle more apparent. Siphonal canal medium sized or long, 29-33% of total shell length, narrow, straight, or weakly abaxially recurved, with 2 or 3, squamous, narrow spiral cords adaperturally.

Uniformly milky-white.

Operculum and radula unknown.

Remarks.

Trophonopsis segmentatus (Verco, 1909) (Fig. 25) has a more convex shell with rounded, crowded spiral cords, more numerous cords on spire whorls, and a smoother shoulder. The spire is higher, and the siphonal canal is markedly shorter, occupying 18% of the total shell length in *T. segmentatus* instead of 29-33%. The aperture of *T. segmentatus* is ovate, with a broad columellar lip, instead of triangular with a narrow columellar lip.

Trophonopsis plicilaminatus (Verco, 1909) (Fig. 24) has fewer, lower spiral cords, a smooth shoulder, and an ovate aperture.

Another species, described from New South Wales, *Trophonopsis simplex* (Hedley, 1903) (Fig. 26) has a smoother, more convex shell with a roundly-ovate aperture. The spire whorls are rounded with more numerous spiral cords (8 or 10 cords on last whorl with a higher density on abapical part of the whorl).

Etymology.

Named in memory of the late Arthur Bassett, Shark Bay, West Australia, whom I have known for many years, and who has sent me many Australian muricids and other Australian shells

Subfamily **ERGALATAXINAE**
Kuroda & Habe, 1971
Genus ***Orania*** Pallary, 1900

Type species (by original designation): *Pseudomurex spadae* Libassi, 1889 (= *Murex fusulus* Brocchi, 1814); Pliocene to Recent, Mediterranean, eastern Atlantic.

Orania rosadoi n.sp.

Figs 27-29, 43

Type material examined.

South Mozambique: Quissico area, ex pisce, in 50-60 m, holotype NM L3374/T1463. Paratypes: 6 NM L3581/T1464; 1 MNHN; 2 coll. J. Rosado of Maputo, 1 coll R. Houart (all dd).

Distribution.

Quissico area, South Mozambique, 50-60 m (ex pisce).

Description.

Shell medium sized for the genus, up to 13.3 mm in length at maturity (paratype NM), slender, weakly spinose, lightly built. Spire high with 1.5 protoconch whorls and up to 5 angulate, shouldered, weakly spinose teleoconch whorls. Suture impressed. Protoconch small, globose; whorls rounded, smooth; terminal varix shallow, thin, weakly curved. Axial sculpture of teleoconch whorls consisting of low, broad, nodose, weakly spinose varices: 8-10 varices from first to penultimate whorl; 7 or 8 on last whorl. Spiral sculpture of high, squamous, primary and secondary cords: 2 on first whorl, 2 or 3 on second and third; 3 or 4 on fourth; 4 or 5 primary cords and 2-4 secondary cords on last whorl; carinal cord forming small, open spines at intersection with axial varices.

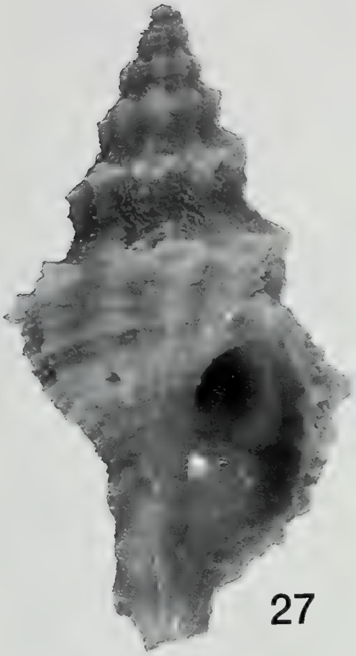
Aperture moderately large, narrow, ovate; columellar lip smooth, rim broken in all specimens; anal notch shallow, broad; outer lip with 6 or 7 elongate denticles within. Siphonal canal short, straight, open, with 3 or 4 spiral cords.

Light brown with darker coloured blotches on suture, and occasionally with darker coloured secondary spiral cords between third and fourth abapical primary cords of last whorl.

Operculum and radula unknown.

Remarks.

The classification of this new species in Ergalataxinae, and in *Orania*, is tentative, as no radula is available.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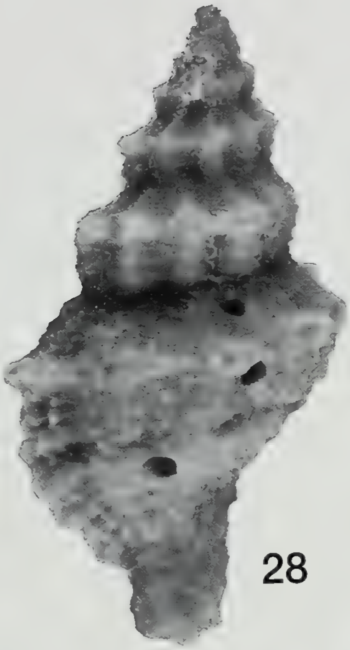
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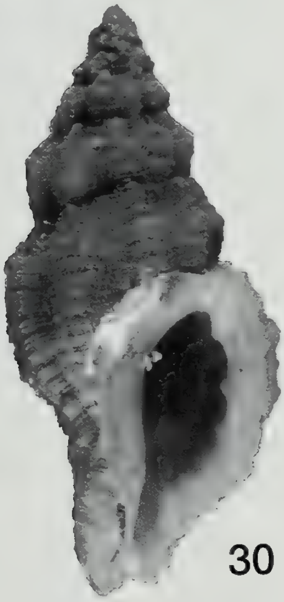
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Figs 27-29. *Orania rosadoi* n.sp. Mozambique, Quissico area. Figs 27-28. Holotype NM L3374/T1463, 11.9 mm. Fig. 29. Paratype NM L3581/T1464, 10.5 mm. **Fig. 30.** *Ergalatax dattilioi* n.sp. Indonesia, Tanimbar Ids, 184-186 m, MNHN, 14.1 mm. **Fig. 31.** *Attiliosa caledonica* (Jousseaume, 1881). Philippine Islands, Mindanao, Balut Id, 200 m, coll. A. Deynzer, 27.7 mm.

Nevertheless, the size, shape, and sculpture of the shell are similar to other species included in the Ergalataxinae, and more particularly in *Orania*. Another possibility might be *Vaughtia* Houart, 1996 (Ocenebrinae), currently known exclusively from southern Africa. However, the shells of *Vaughtia* species are usually more rounded, with lower axial sculpture or none, and a broader aperture.

Orania rosadoi n.sp. resembles *O. mixta* Houart, 1995, but has fewer and broader, secondary spiral cords on last teleoconch whorl, and a paucispiral protoconch of 1.5 whorls, whereas *O. mixta* has a multispiral, conical protoconch of sinusigera type, with 3.5 whorls. Adults of *O. rosadoi* also seems to have a constantly smaller size than *O. mixta*.

Orania rosadoi n.sp. differs from *O. adiastolos* Houart, 1995, another species with paucispiral protoconch, currently known from Zululand (South Africa), and New Caledonia, in having a narrower, more shouldered shell, with fewer secondary spiral cords on last whorl, and elongate denticles within the outer lip, rather than lirae.

Etymology.

Named for Mr. J. Rosado, Maputo, who donated the type material.

Genus *Ergalatax* Iredale, 1931

Type species (by original designation): *Ergalatax recurrens* Iredale, 1931 (= *Murex pauper* Watson, 1883); Recent, Indonesia.

Ergalatax dattilioi n.sp.

Figs 30, 35-37, 44, 45

Cytharomorula sp. - HOUART, 1986: 432, pl. 5, fig. 19 (holotype illustrated).

Ergalatax tokugawai - HOUART, 1997: 290 (not *Ergalatax tokugawai* Kuroda & Habe, 1971).

Type material examined

Philippine Islands: 13°57' N, 120°16' E, 150-159 m, holotype MNHN (lv.); Cebu, Mactan Island, 73-110 m, in coral, 1 paratype coll. R. Houart (lv.).

Other material examined.

Philippine Islands: Mactan Island, Punta Engaño, approximately 50 m, coll. F.J. Springsteen (2 lv.).
Indonesia: Tanimbar Islands, 07°59' S, 133°02' E, 184-186 m, MNHN (2 lv., 1 dd); 08°00' S, 132°59' E, 206-210 m, MNHN (4 dd).
Japan: Wakayama Pref., Minabe, 100-120 m, coll. R. Houart (1 lv.).

Distribution.

Tanimbar, Indonesia, the Philippine Islands, and South of Japan, taken alive at 50-186 m (Fig. 45)

Description.

Shell small sized for the genus, up to 17.7 mm in length at maturity, slender, tuberculate. Spire high with 3+ protoconch whorls and up to 6 weakly angulate, shouldered teleoconch whorls. Suture impressed. Protoconch conical, acute, smooth, glossy, of sinusigera type. Axial sculpture of teleoconch whorls consisting of high, strong, nodose ribs: 8 on first whorl, 8 or 9 on second, 8-10 on third, 9-11 on fourth and fifth, 7-9 on last whorl. Spiral sculpture of low, nodose, broad cords, covered by narrow, occasionally shallow threads: 2 or 3 cords on first whorl, 2 or 3 cords on second whorl, and 1 thread on shoulder, 2 or 3 on third with 1 thread and 3 or 4 threads on shoulder, 2 or 3 on fourth with 4 threads and 4-6 threads on shoulder, 3 on fifth with 16-18 threads and 8-12 threads on shoulder, 6-9 cords on last whorl with numerous threads and 12-15 threads on shoulder.

Aperture large, ovate; columellar lip smooth, occasionally with 1 or 2 low, weak knobs abapically. Rim adherent, weakly erect abapically; anal notch narrow, deep; outer lip erect, smooth, with 5 or 6 weak or strong elongate denticles within. Siphonal canal short, broadly open, with some narrow threads.

Light tan or light brown, occasionally with some weakly darker coloured blotches on axial ribs, and occasional darker coloured threads between spiral cords. Aperture white.

Operculum and radula unknown.

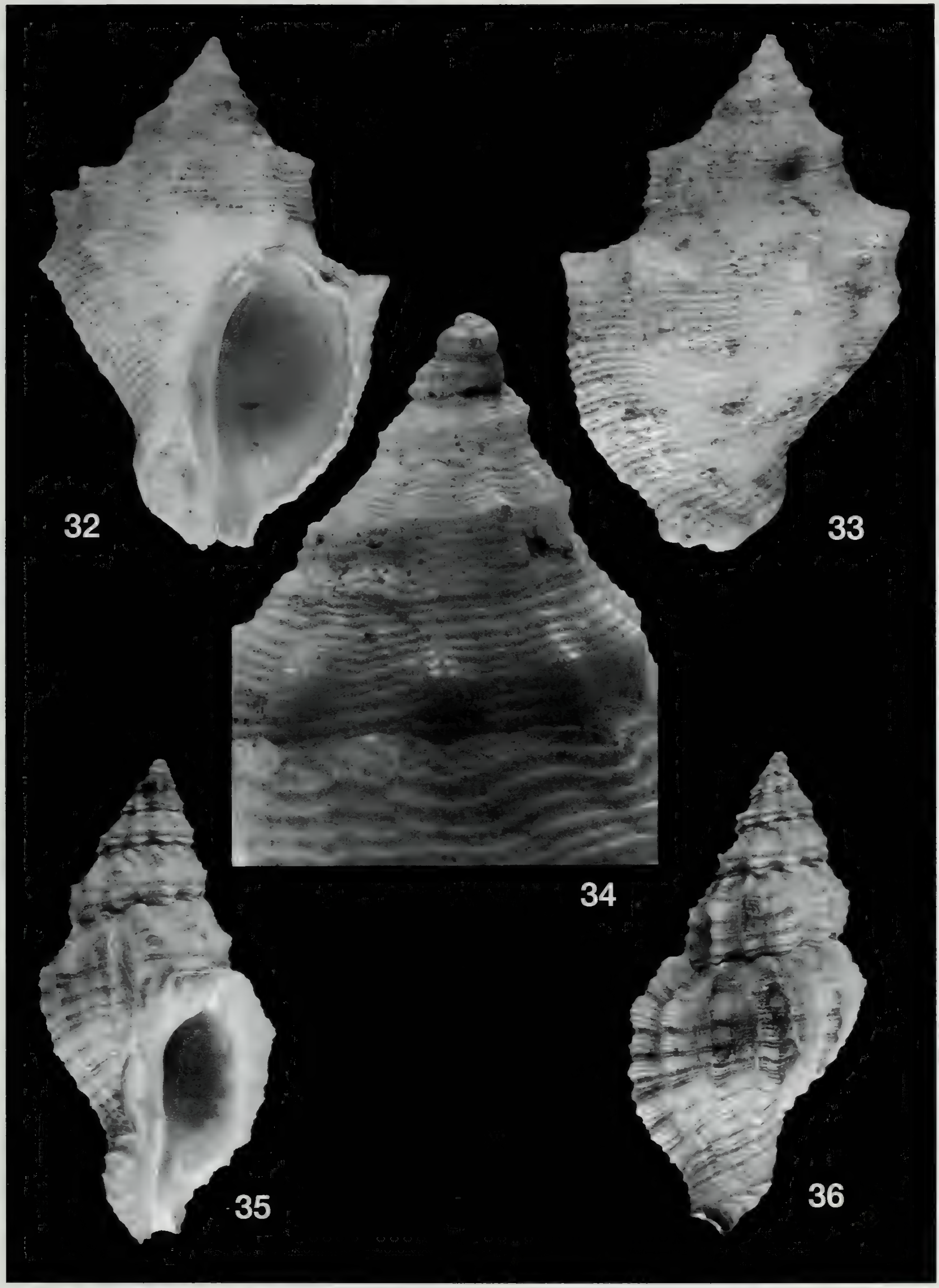
Remarks.

Ergalatax dattilioi was recently identified as *E. tokugawai* (HOUART, 1997), but from comparison on type material (holotype, Figs 38-39) they are clearly distinct species. *E. dattilioi* has more elongate teleoconch whorls, and different spiral sculpture. In *E. dattilioi* the spiral cords are broad and covered with narrow threads, in *E. tokugawai*, the spiral cords are narrow, smooth, with 2 or 3 threads between each pair of cords. The spiral threads are more numerous, and narrower in *E. dattilioi*.

The genus *Cytharomorula*, once used for the species (HOUART, 1986), resembles *Ergalatax* although having shells with more adpressed suture, higher last teleoconch whorl, and shorter siphonal canal relative to the shell length.

Etymology.

Named in memory of the late Anthony D'Attilio, San Diego, California, known throughout the world for his numerous papers on Muricoidea.



Figs 32-34. *Thais (Mancinella) herberti* n.sp. Figs 32-33. South Africa, northern Natal, off Glenton Reef, 110 m, holotype NM S2603/T1465, 31.1 mm. Fig. 34. Protoconch and first whorls. **Figs 35-36.** *Ergalatax dattilioi* n.sp. Philippine Islands, 13°57' N, 120°16' E, 150-159 m, holotype MNHN, 16.2 mm.

Subfamily **RAPANINAE** Gray, 1853
Genus *Thais* Röding, 1798
Subgenus *Mancinella* Link, 1807

Type species (by absolute tautonomy, ICZN, opinion 911): *Mancinella aculeata* Link, 1807 (= *Volema alouina* Röding, 1798); Recent, Indo-West Pacific.

Thais (Mancinella) herberti n.sp.

Figs 32-34, 41-42

Mancinella cf. *siro* (Kuroda, 1931) - LUSSI & BRINK, 1996: 3, fig. 17.

Type material examined.

South Africa: Northern Natal, off Glenton Reed, 29°13.7' S, 32°02.0' E, 110 m, sponge, holotype NM S2603/T1465 (lv.); Natal, off Scottburgh, 100 m, 1 paratype NM B3485/T1466 (lv.).

Other paratypes: off Port Shepstone, 70 m, eroded shell + sponge rubble, 1 NM B3665/T1467 (dd); Zululand, N.E. of Gipsy Hill, 27°45.2' S, 32°39.8' E, 110 m, sponge, stones, 1 NM E3731/T1468 (lv.); Zululand, off Richards Bay, 28°59' S, 32°11' E, 100 m, 1 NM B6313/T1469 (lv.); 1 coll. R. Houart (lv.); Zululand, off Matigulu R. mouth, 29°17.1' S, 31°50.3' E, 50 m, mud, 1 NM V5136/T1471 (lv.); Zululand, off Matigulu Bluff, 29°21.4' S, 31°56.2' E, 90 m, sponge, 1 NM E8760/T1470 (lv.).

Distribution.

Natal and Zululand, South Africa, taken alive at 50-110 m, on sponge bottoms on mid-continental shelf.

Description.

Shell small for the subgenus, up to 34 mm in length at maturity (paratype NM E8760/T1470), heavy, biconical. Spire high, with 2+ protoconch whorls (partially broken), and up to 5 or 6 broad, convex, shouldered teleoconch whorls. Suture adpressed. Protoconch large, conical; whorls rounded, minutely punctate, with a narrow keel abapically. Terminal varix of sinusigera type. Axial sculpture of teleoconch whorls consisting of low, broad, weakly spinose ribs, each with one short, acute, broad spine on shoulder. Last whorl with 2 rows of short spines. First whorl with 10-12 axial ribs, second with 10, third, fourth and fifth with 9 or 10, last whorl with 7 or 8 ribs. Spiral sculpture of high, strong, squamous, primary and secondary cords: first whorl with 3 cords on whorl and 2 on shoulder, second with 3 on whorl, 4-6 on shoulder, third and fourth with 6 on whorl, 9 on shoulder, fifth whorl with 8 or 9 on whorl, 12 or 13 on shoulder, last whorl with 27 on whorl, 14-17 on shoulder.

Aperture large, broad, ovate; columellar lip smooth, adherent, weakly detached abapically; anal notch broad; outer lip crenulate, with 8-10 strong lirae within. Siphonal canal short, broad, straight, broadly open, with 5 or 6 primary and secondary, rounded spiral cords.

Light tan, aperture white.

Operculum dark brown, D-shaped, with lateral nucleus in center right. Radula with a long, broad central cusp; lateral cusps with inner lateral denticles; 3 or 4 marginal folds or weak denticles. Lateral teeth long, broad.

Remarks.

Thais (Mancinella) echinata (Blainville, 1833) differs primarily in having a more rounded shell with 4 spiral rows of short, acute spines on the last teleoconch whorl; its aperture is relatively smaller with more numerous, weaker lirae and broader columellar lip, with a less well delimited edge. The Japanese species *T. siro* (Kuroda, 1931) has 4 spiral rows of short spines, a more indistinct edge of columellar lip, more flattened spiral cords on the last teleoconch whorl, and 4 low, weakly elongate nodes within the outer apertural edge instead of 8-10 lirae. At first sight, the shell also resembles *Drupella cornus* (Röding, 1798) and *D. eburnea* (Küster, 1862), but both species are narrower, have fewer, broader spiral cords, a denticulate instead of lirate outer apertural lip, a narrower aperture, and a higher spire. Moreover, the radula of *Drupella* is quite different from that of *Thais*, and from other rapanines, in having long and slender, reed-shaped laterals.

Etymology.

Named for Dr. Dai Herbert (Natal Museum, Pietermaritzburg), known for his numerous papers on South African Trochoidea, and who took the beautiful photograph of *T. herberti in situ*.

ACKNOWLEDGEMENTS. This study was made possible thanks to the helpful collaboration of many people. For the material I am thankful to P. Bouchet (Muséum National d'Histoire Naturelle, Paris); P. Clarckson (Port Lincoln, South Australia); A. Deynzer (Sanibel, Florida); A. Edinger (Mandurah, Western Australia); R.N. Kilburn (Natal Museum, Pietermaritzburg), and I. Loch and W.F. Ponder (Australian Museum, Sydney). Many thanks also to K. Hasegawa (Showa Memorial Institute, Tsukuba, Japan), and to T. Okutani (Nihon University, Kanagawa-ken, Japan) for helpful information and for the loan of Kuroda's type specimens. I am also much indebted to A. Warén (Naturhistoriska Museet, Stockholm, Sweden) for processing and SEM of the radulae, and to B. A. Marshall (Museum of New Zealand, Wellington) and E.H. Vokes (Tulane University) for their constructive comments, suggestions, and linguistic assistance.

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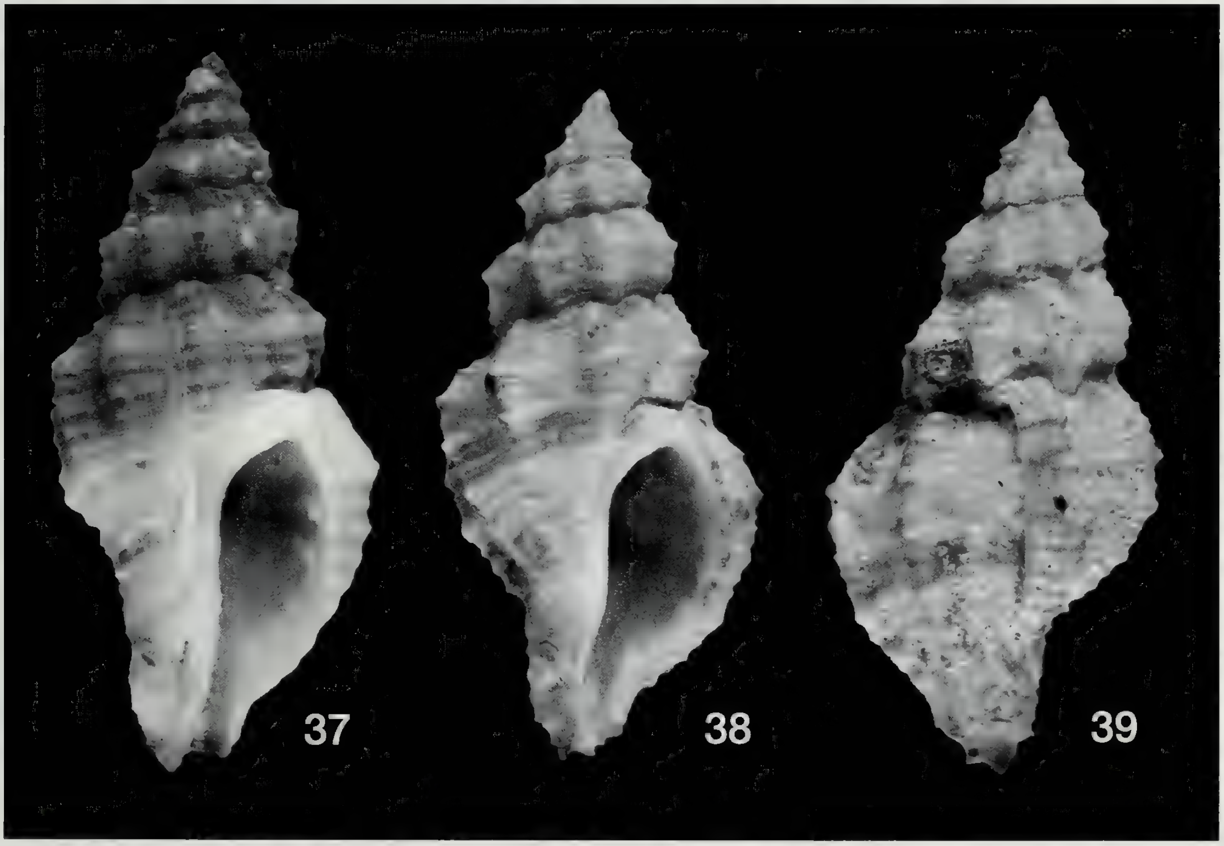
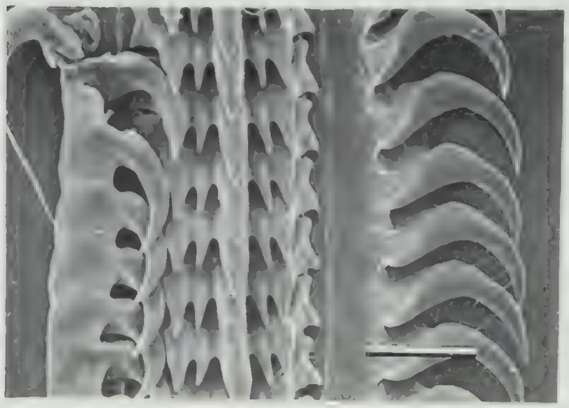


Fig. 37. *Ergalatax dattilioi* n.sp. Japan, Wakayame Pref., Minabe, 100-120 m, coll. R. Houart, 17.7 mm. **Figs 38-39.** *Ergalatax tokugawai* Kuroda & Habe, 1971. Japan, Miura Peninsula, Kanagawa Pref., WS, 2 km off Jōgashima, 78-85 m, holotype NSMT-MOR 9604, 16 mm.



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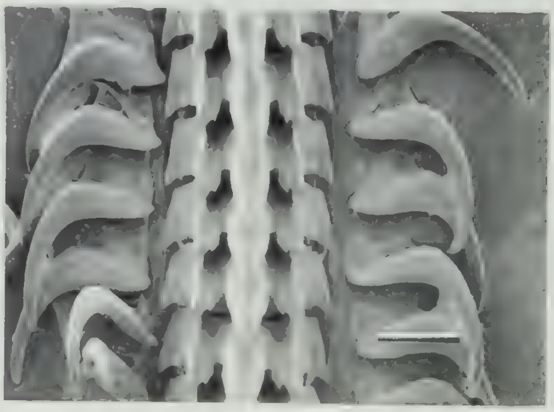

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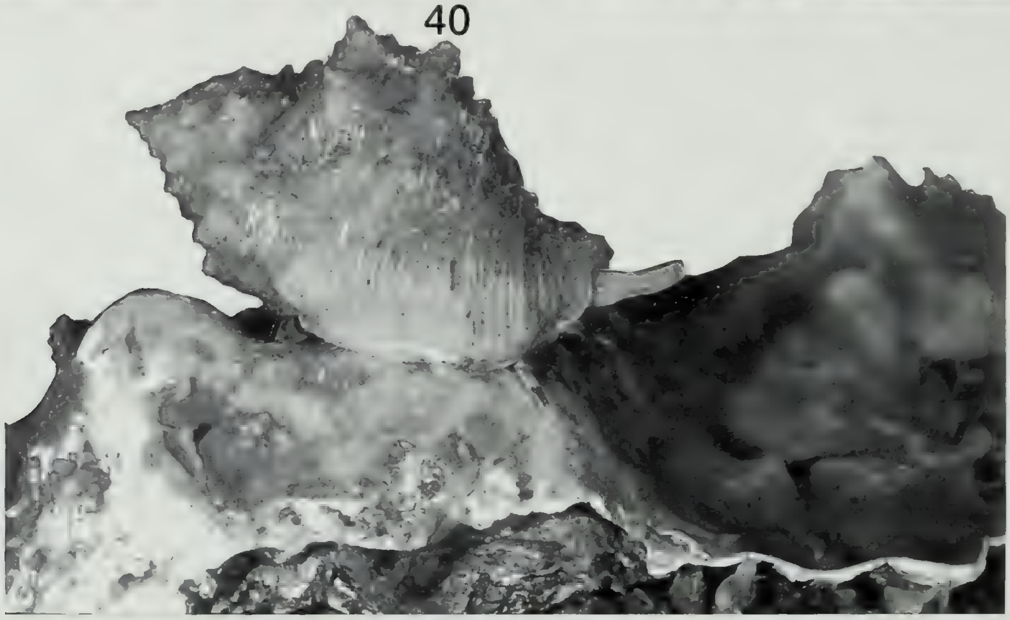

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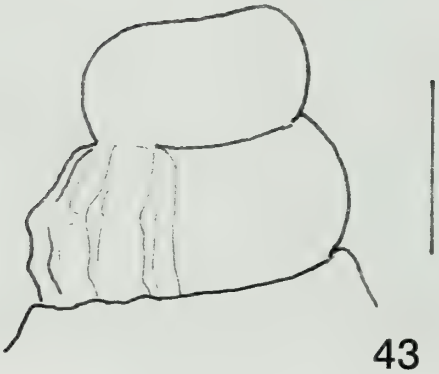

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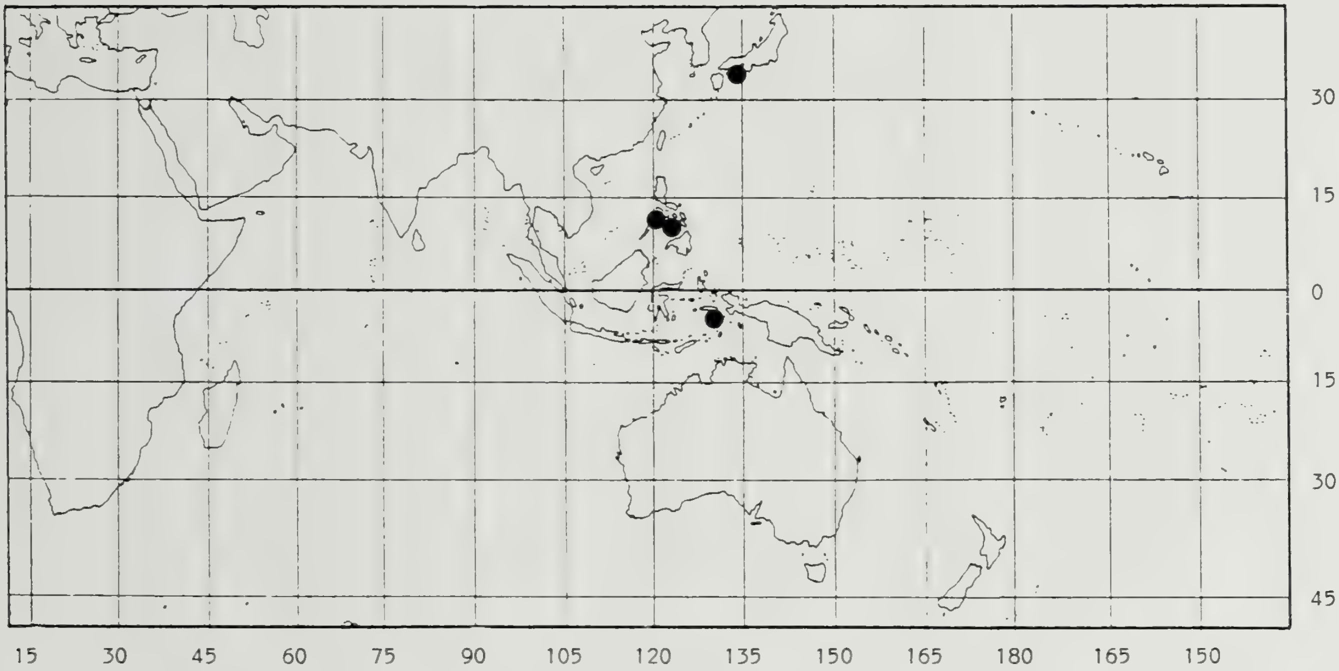
Figs 40-41. Radulae (scale bar: 50 µm). Fig. 40. *Attiliosa edingeri* n.sp. West Australia, off Esperance. Fig. 41. *Thais (Mancinella) herberti* n.sp. South Africa, Zululand. **Fig. 42.** *Thais (Mancinella) herberti* n.sp. *In situ*, on sponges, paratype NM E8760/T1470, photo D. Herbert. **Figs 43-44.** Protoconchs (scale bar: 0.5 mm). Fig. 43. *Orania rosadoi* n.sp. Fig. 44. *Ergalatax dattilioi* n.sp.



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Figs 45-47. Distribution maps. Fig. 45. *Ergalatax dattilioi* n.sp. Fig. 46. *Apixystus rippingalei* n.sp. Fig. 47 *Trophonopsis bassetti* n.sp.

Taxonomic revision of the Indo-Pacific *Vasticardium assimile* species group (Mollusca, Cardiidae)

Jacques VIDAL

Attaché au Museum National d'Histoire Naturelle de Paris,
Laboratoire de Malacologie, 55 rue Buffon, 75005 Paris, France

KEYWORDS. Mollusca, Bivalvia, *Vasticardium*, Indo-Pacific.

SUMMARY. Several forms of Indo-Pacific *Vasticardium* of medium size, are here grouped as the *Vasticardium assimile* species group. Three of these forms, mainly from the Indian Ocean and previously described as three different species, *V. assimile*, *V. lacunosum* and *V. rubicundum*, share many characters and have often been confused. They are considered here to represent only two species, *V. assimile* and *V. rubicundum*, while *V. assimile lacunosum* is treated as a subspecies restricted to the Persian Gulf. *V. assimile* is restricted to the western Indian Ocean, southernmost Red Sea and Persian Gulf, whereas *V. rubicundum*, although more abundant in the southeastern Indian Ocean, extends also into a large part of the western Pacific, where it has been described as *mindanense*, *compunctum*, and *kengaluorum*. Two rare additional species, *Vasticardium rhegminum*, from the Masirah area (Oman), and *Vasticardium thomassini* sp. nov., from southeastern Africa and Madagascar, are treated.

MATERIAL, METHODS AND TEXT CONVENTIONS

The material comes from the following museums:

AMS: Australian Museum, Sydney.
ANSP: Academy of Natural Sciences, Philadelphia.
BMNH: The National History Museum, London.
IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels.
LACM: Los Angeles County Museum of Natural History, Los Angeles.
MHNG: Museum d'Histoire Naturelle de Genève, Geneva.
MNHN: Museum National d'Histoire Naturelle, Paris.
NHMW: Naturhistorisches Museum, Vienna.
NMW: National Museum of Wales, Cardiff.
RMNH: Nationaal Natuurhistorisch Museum, Leiden.
USNM: National Museum of Natural History, Washington.
ZMA: Zoologisch Museum, Amsterdam.
ZMUC: Zoologisk Museum, Copenhagen.

In the description of the shells, particular attention was devoted to the rib morphology (structure and ornamentation of the ribs), this in an ontogenic perspective, by taking into account these elements in the earliest parts of the shell and their variations towards the adult parts, in the various "quarters".

For examination purposes, the shells are divided externally into four radial "quarters": **AQ**: Anterior Quarter; **MAQ**: Medio-Anterior Quarter; **MPQ**: Medio-Posterior Quarter; **PQ**: Posterior Quarter. Longitudinally, shells are divided schematically into two parts, a "juvenile" (or umbonal) part and an "adult" (or marginal) part. In the description of the hinges, angle **A** is the angle formed by the two lines joining the tip of the main cardinal tooth to the tips of the laterals respectively. Ratio **D** is determined by dividing the length of the line from the tip of the umbo to the tip of the posterior lateral by the corresponding distance from the umbo to the tip of the anterior lateral.

SYSTEMATICS

Family **CARDIIDAE** Lamarck, 1809

Genus ***Vasticardium*** Iredale, 1927.

Type species: *Cardium elongatum* Bruguière, 1789, by original designation, Iredale 1927: 75.

Diagnosis. Shells medium to large, generally elongated and variably inflated. Shape ovoid and symmetrical or posteriorly expanded, obliquely or not, "winged" or truncated. Mean rib number ranges from 30-40, exceptionally 45. Hinge line moderately angled (Angle A circa 130°). Cardinal teeth in right valve separated or merely touching at their base and never connected by a high and narrow dorsal saddle.

In juvenile median and anterior parts, ribs quickly become high, square-sided and fully ornamented, directly following millimetric smooth, very primitive shell. In PQ, ribs always high and square-sided, always simple, not longitudinally divided into two parts; top scales or nodules always arranged in a single row along apex. In other quarters of adult shells, ribs generally high, often squared and overhanging interstices, rarely triangular; in MPQ they often bear scales or tubercles with crenulated margins, cross-bars in the anterior half. Interstices moderately deep and wide, with a smooth or finely striated flat bottom, independent from flanks of ribs.

Remark. In previous papers (VIDAL, 1992, 1993), I provisionally used *Acrosterigma* Dall, 1900, for species belonging to the same genus as the one described here. I currently consider the genus *Vasticardium*, as defined above, to be more appropriate.

DIAGNOSIS OF THE *VASTICARDIUM ASSIMILE* SPECIES GROUP

Species of the group, all of medium size, share several similar macroscopic characters such as shape, hinge structure, rib number, and above all color. In addition, the young shells (up to one or two cm in height or slightly more) are somewhat similar as far as rib sculpture is concerned: in PQ, rather low, asymmetrical ribs bearing top oblique scales, with a sharp anterior margin overhanging interstices (Fig. 8) and, in other parts of shell, high ribs with a roundly triangular top zone crenulated on margins which often overhang smooth and flat-bottomed interstices (Figs 6-7).

Another significant similarity is that the carbonates which form the shell seem to have a characteristic thin microscopic structure which makes the shell fragile, and easily faded, worn or notched, and gives it lustreless colorations. In addition, ribs are constituted of several carbonaceous laminae, longitudinally juxtaposed, some of them with pink coloration visible when ribs are worn.

Vasticardium assimile (Reeve, 1844)

Figs 1-11, 25-26.

Cardium assimile Reeve, 1844, Sp. 45, pl. 9, fig. 45.
Cardium lacunosum Reeve, 1845, Sp. 81, pl. 16, fig. 81.

Selected references.

Cardium assimile: Römer, 1869, pl. 11, fig. 11.
Cardium assimile: Braga, 1952: 49, pl. 10, fig. 2.
Laevicardium (Trachycardium) rubicundum: Fischer-Piette, 1977: 65 [Partly].
Trachycardium lacunosum: Bosch, 1982: 172.
Trachycardium lacunosum: Smythe, 1982: 100, pl. 18, fig. c.
Trachycardium elongatum: Drivas & Jay, 1988: 140, pl. 55, fig. 1.
Trachycardium lacunosum: Oliver, 1992: 126, pl. 23, fig. 8a-b.
Acrosterigma assimile: Oliver, 1995: 246, fig. 1091.
NOT *Trachycardium lacunosum*: Keen, 1945: 36 [= probably *rubicundum*].

Type material.

Cardium assimile : Three syntypes in BMNH Reg. N° 1978-129, from Zanzibar. The largest is figured here (Figs 1-3). Another specimen corresponds exactly to the dimensions of Reeve's figure (H= 56.0, L= 42.7 mm), but looks different because the illustration is of poor quality.

Cardium lacunosum: One shell considered as holotype in BMNH Reg. N° 1978-133 locality unknown (Figs 4-5). The right valve fits the figured one as far as dimensions and rib number are concerned, but several other characters do not match Reeve's figure and description. For example, ribs are curved backwards in projection with thin numerous marginal crenulations (at least 40: see definition p. 11-2) in the supposed "holotype", as opposed to perfectly straight ribs with strong rarer crenulations (barely 20 in number) in Reeve's specimen. For these reasons I think that the shell in the BMNH, which is a "common" form of *V. assimile*, is not the shell described and figured by Reeve as *lacunosum* [which means "hollowed", an allusion to the strong marginal crenulations of the ribs; Reeves writes "laterally hollowed"], and a neotype will be selected for these special forms from the Persian Gulf considered as a subspecies: *V. assimile lacunosum* (see below).

Description.

Shells medium to large. Shape regularly subovoid, almost equilateral but somewhat posteriorly truncated, with ribs sometimes slightly curved backwards in projection. Generally elongated in the adult stage (mean L/H= 0.77; range 0.71-0.92), and relatively tumid (mean W/L= 0.87; range 0.79-1.02).

Lunule narrow but well marked, and purple in color. *V. assimile* is always externally colored with stripes and/or splashes of vivid but lusterless brown or purple, more rarely orange or pink; interior white, sometimes with a double colored ray in umbonal area, and purple margin.

Figs 1-3. *Vasticardium assimile*, Syntype, BMNH 1978-129, L= 47.0 mm. **Figs 4-5.** *Vasticardium assimile*, specimen erroneously considered as holotype of *Cardium lacunosum* Reeve, BMNH 1978-133, L= 40.5 mm. **Figs 6-7.** *Vasticardium assimile*, specimen from Magaruque Is, Mozambique, MNHN. Fig. 6: left valve; detail of juvenile median part of shell; scale x 5. Fig. 7: right valve; detail of juvenile PQ and MPQ; scale x 5. **Fig. 8.** *Vasticardium assimile*, right valve, specimen from Zanzibar, MNHN; detail of juvenile MPQ and MAQ, particularly thin and numerous marginal crenulations on the ribs (50 per two cm); scale x 2.5.

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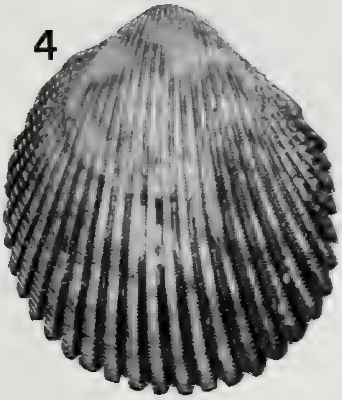

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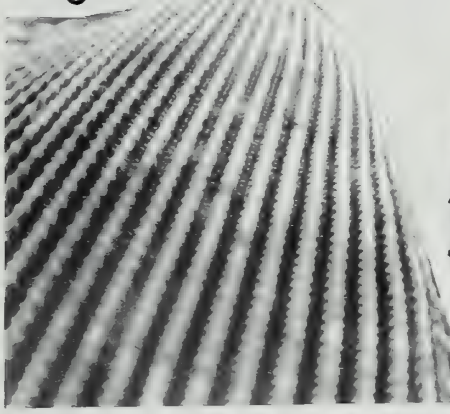

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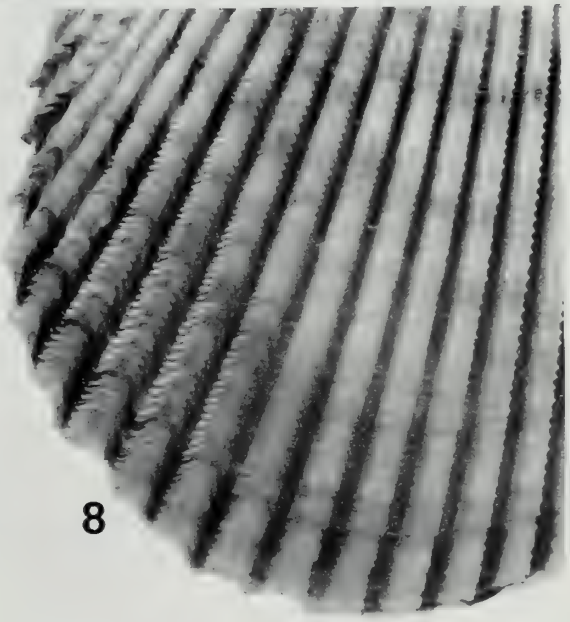

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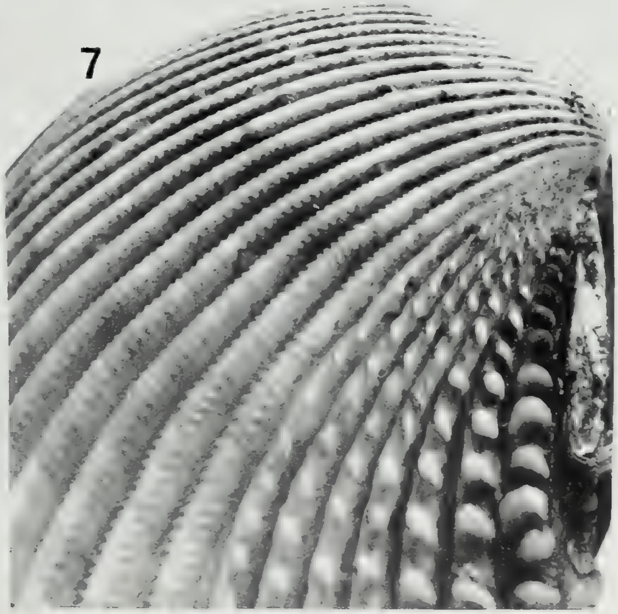

Hinge moderately arched (mean < A= 130°, range 120-135°) and rather asymmetrical (mean ratio D= 1.20, range 1.00-1.45). Posterior cardinal tooth in left valve long (2/3 of the width of the hinge area) and high (almost as high as main cardinal), relatively narrow and often with an acute summit. Foundation of anterior lateral (mainly in left valve, tooth PII) very moderately "hook-shaped". A medial short weak rib (umbonal support) present in umbonal cavity of many shells.

Mean rib number 33.4 (range 31-37).

Rib morphology:

In juvenile PQ (Fig. 8) ribs rather low and asymmetrical, with anterior edge overhanging interstice, with a sharp continuous margin jutted in front of scales. Rib tops set with large, more or less tubercular, slightly twisted oblique scales; no secondary small scales occur on edges of ribs as in some other species groups of *Vasticardium*; interstices as wide as ribs. In adult PQ, scales on rib tops can become more or less rounded tubercles, often irregular in shape and degenerate.

The juvenile median part of shell (Fig. 6) bears high ribs, of trapezoidal section with wide sloping flanks and a slightly rounded smooth top zone, bordered on both sides by crenulations which overhang the flanks; tops sometimes regularly swollen by extension of marginal crenulations. Interstices also trapezoidal in section, and almost as large as ribs; their bottoms are flat and clearly separated from flanks of ribs by a break line. This bottom often transversely very finely notched and flanks sometimes distinctly grooved, mainly posteriorly. In adults, a significant change from the juvenile sculpture occurs in MPQ (Fig. 25): the last ribs of this quarter (close to PQ) become very asymmetrical with anterior flank shorter and more abrupt; on anterior margins of ribs, the crenulated projecting edge does not change, but on the wider posterior side, marginal crenulations progressively join the flank ridgelets which become stronger, and overhanging disappears. Posterior parts of ribs form a wide dipping flank, entirely strongly ridged, ridges and furrows becoming more and more irregular with age; this evolution (illustrated in Fig. 25) is very characteristic of *Vasticardium assimile* and examining it always allows to separate this species. The reduced rib tops remain smooth or become regularly ridged in the most adult part, rarely with a herringbone structure. In anterior part of adult MPQ and MAQ, ribs remain crenulated on both overhanging margins.

In juvenile AQ, ribs more square-sided, and slightly asymmetrical, with transverse ridges on their top (Fig. 6); interstices rounded, without any discontinuity with rib flanks, both being slightly striated by fine growth lines. In adult AQ, tops of ribs become flat and depressed anteriorly and are ornamented with slightly curved, strong imbricated cross-bars.

Material examined.

The following lots in addition to the type material:

A) South Africa: East London: 1(MNHN); Port Sheptone: 1(MNHN), 1(ANSP)

B) Mozambique: Magaruque Island: 1(MNHN); Santa Carolina Island: 2(MNHN); no specific location: 1(MNHN)

C) Madagascar: Tulear: 2(MNHN); no specific location: 1(MNHN), 1(BMNH)

D) TANZANIA: Zanzibar: 5(MNHN), 2(BMNH), 1(ANSP), 1(USNM), 1(LACM); M'Boa Maji: 1(USNM)

E) Kenya: Shimoni: 1(BMNH); no specific location: 1(MNHN)

F) Somalia: Eil: 1(MNHN); Beidi: 1(MNHN); Mogadishu: 1(MNHN), 1(ANSP); S. Cape Guardafui: 1(MNHN); Bender Kassim: 1(MNHN); W. Elayu: 1(MNHN); E. Sugra: 1(MNHN); Mait: 1(MNHN); Candara: 1(ANSP)

G) Aden: 1(MNHN); 1(BMNH)

H) Djibouti: 2(MNHN)

I) Yemen: Abd el Kuri Island: 1(MNHN); Socotra Island: 1(MNHN); Mocha: 1(MNHN); Hodeida: 2(MNHN), 2(USNM); N. Hodeida: 1(MNHN)

J) Oman: Masirah: 1(MNHN); Musqat: 1(MNHN); 1(BMNH)

K) Persian Gulf: Bender Abbas: 1(MNHN); Khassab: 1(BMNH); Trucial Coast: 2(BMNH); Lavan Is: 1(MNHN); Al Hamra: 1(MNHN); Doha: 1(MNHN); Dammam: 1(USNM); Ras Tannurah: 2(ANSP), 1(USNM); Kuwait, Al Fintas: 1(MNHN); Kuwait: 1(USNM); not localized: Tarut Bay: 1(ANSP), 1(USNM); Chaschuse Is 1(USNM); no specific location: 1(BMNH); 1(LACM)

L) Pakistan: Karachi: 1(BMNH), 1(USNM)

M) India: Tuticorin: 1(MNHN); Gulf of Manaar: 2(ANSP), 1(BMNH)

N) Sri Lanka, Trincomalee: 1 (BMNH); no specific location: 2(BMNH); 2(USNM); 1(LACM)

O) No locality: 3(MNHN).

Figs 9-11. *Vasticardium assimile* lacunosum, Neotype, MNHN, ex coll. Vidal, L= 46.0 mm. **Figs 12-14.** *Vasticardium rubicundum*, Syntype, BMNH ex coll. Cuming, L= 49.0 mm. **Figs 15-17.** *Vasticardum rhegminum*, bivalved specimen, MNHN ex coll. Sue Hobbs, L= 39.4 mm. **Figs 18-19.** *Vasticardium rubicundum*, Lectotype of *Cardium mindanense*, BMNH 1070-124, L= 34.7 mm. **Fig. 20.** *Vasticardium rubicundum*, Paralectotype of *Cardium mindanense*, BMNH 1070-124, L= 34.0 mm. **Figs 21-24.** *Vasticardium thomassini*, Holotype, MNHN ex coll. Thomassin, L= 27.7 mm.

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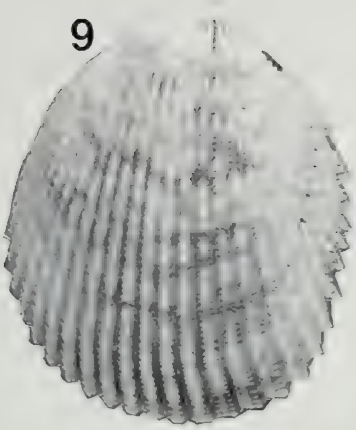

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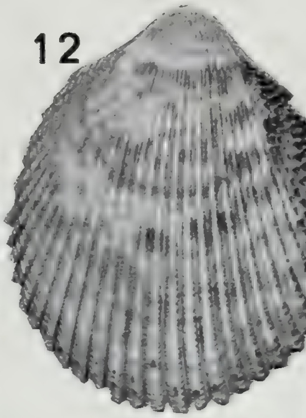

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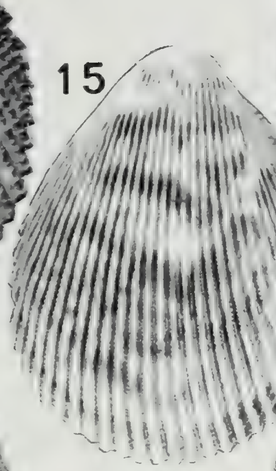

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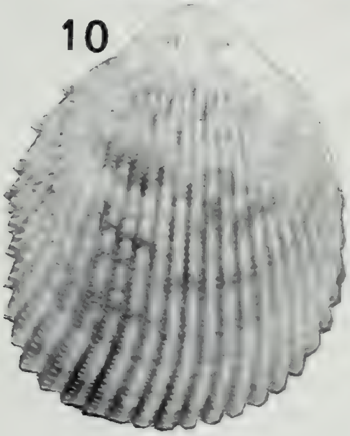

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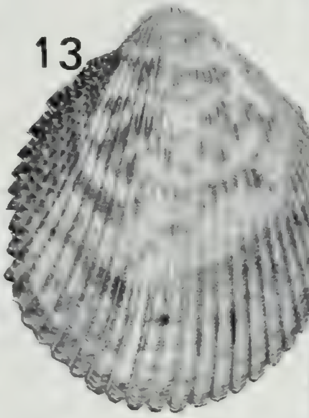

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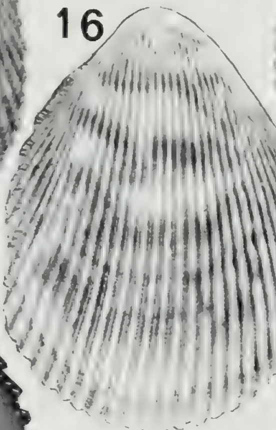

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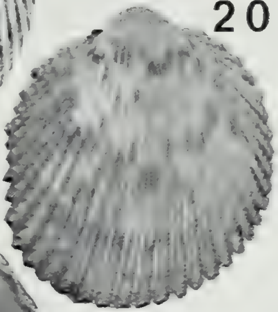

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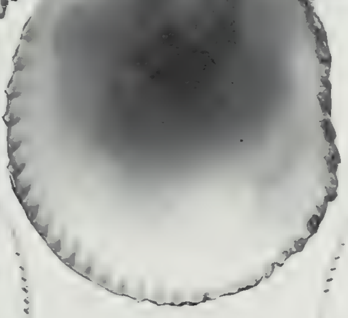

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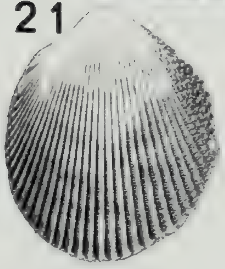

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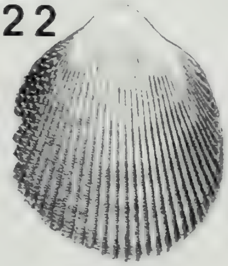

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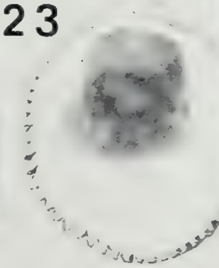

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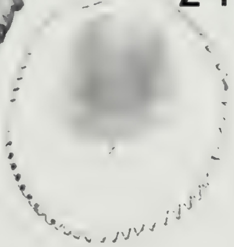


Measurements of *V. assimile ss*, excluding Persian Gulf forms.

	Height	**Length**	**Width**	**L/H**	**W/L**	**ratio D**	**angle A**	**Ribs**
	(mm)	(mm)	(mm)				°	
Syntype	63.3	47.0	40.0	0.74	0.85	1.15	120	33
Syntype	56.0	42.7	35.3	0.76	0.83	1.20	120	34
Mozambique	53.7	40.0	34.4	0.74	0.86	1.27	125	35
Madagascar	57.0	47.0	41.3	0.82	0.88	1.05	130	34
Zanzibar	59.4	44.3	37.2	0.75	0.84	1.15	120	34
Kenya	47.4	35.5	30.6	0.75	0.86	1.25	125	34
Socotra Is.	53.2	40.6	34.0	0.77	0.84	1.14	125	34
N Somalia	42.1	30.2	28.2	0.72	0.93	1.17	125	36
Aden	44.0	35.8	29.3	0.81	0.82	1.31	125	33
Djibouti	39.0	31.0	24.6	0.79	0.79	1.15	130	32
N Yemen	48.9	34.5	32.1	0.71	0.93	1.26	120	32
Masirah Is	55.8	43.8	36.4	0.78	0.83	1.09	125	32
S India	44.9	36.5	31.2	0.81	0.85	1.60	135	33

The maximum size observed in the "nominal" form is a right valve from Madagascar, in MNHN (H= 68.8 mm, L= 49.0 mm).

Distribution.

Because of the possible confusion with *V. rubicundum*, it is impossible to accept literature records uncritically. From material examined, I have ascertained the following distribution: east coast of Africa from East London (Natal) to the Gulf of Aden, Madagascar, Seychelles, southernmost part of the Red Sea (Yemen), Oman (Masirah, Muscat), Persian Gulf (from Strait of Hormuz as far as Kuwait), Pakistan (Karachi), south India (Gulf of Mannaar), and Sri Lanka.

It is also present in Réunion and Mauritius (DRIVAS & JAY, 1988, pl. 55, fig. 1, under the name *elongatum*). The only record in the literature of *V. assimile* outside these areas is from Java (ALTENA, 1945: 150). There are records of *V. lacunosum* from Torres Strait (MELVILL & STANDEN, 1899: 190) and New Guinea (KEEN, 1945: 36). I consider all these records to probably refer to *V. rubicundum* which has a western Pacific extension.

Remarks.

Differences from *V. rubicundum*: *V. assimile* is very close to *V. rubicundum*, mainly in the juvenile shells. For differences see under *V. rubicundum*.

Variability of *V. assimile*: This species has many constant characters always allowing one to separate it from the others, both within the present group and outside it [It is, particularly, easily separable from *Acrosterigma magnum* (Linné), although it is considered by Reeve "quite similar" (= *assimile*) to this species]. Nevertheless some characters can vary according to populations and/or individuals. The most significant of these variations are:

1- Elongation in adult specimens (L/H range 0.71-0.92).

2- Size and number of the marginal crenulations of the ribs: These are very variable mainly in the median part of the shell, from very small and reduced to thin scales [in which case the ribs in the median part remain roughly triangular and the interstices opened and wide (Figs 8, 25)], to as wide as about half the width of the rib [in which cases the crenulations overhang the flanks of the ribs which are nearly "vertical", and the interstices are reduced in width (Fig. 26)]. Apparently in relation to the size, the number of the crenulations is also variable: in the middle of the shell, in a band between 3 and 5 cm from the tip of the umbo (curved distance), this number varies from 21 to 52.

3- Regular swelling or ridging of the tops of the ribs in the median part of the shell: In the anterior part of the shell, the rib tops always bear cross bars joining the lateral crenulations; this phenomenon gradually disappears backwards and, in the medial part of the shell, the tops can either still be swollen or become flat and smooth. This character varies also with the age of the shell, and the swelling of the tops is variable according to individuals, the young shells developing it relatively late.

4- Shape and size of the top ornaments of the ribs in PQ: These ornaments can vary in the same individual, and also become locally irregular and degenerate; they vary from nodular or elongated tubercles to thin, variably twisted, oblique lamellar scales.

These variations generally occur at random and separately according to populations and/or individuals. However a geographical group with constant simultaneous variations is present in the Persian Gulf, and is here defined as a subspecies: *V. assimile lacunosum*.

Vasticardium assimile lacunosum
(Reeve, 1845)
Figs 9-11, 26.

Cardium lacunosum Reeve, 1845, Sp. 81, pl. 16, fig. 81.

Acrosterigma lacunosa: Oliver, 1995: 246, fig. 1090.

Type material.

As seen above, the specimen BMNH 1978-133 is closer to the nominal subspecies of *V. assimile* and is certainly not the holotype of *C. lacunosum* figured and described by Reeve. Considering that this latter shell is not traced, a neotype of *Cardium lacunosum* is selected here (Figs 9-11), a shell from Al Fintas, Kuwait, in MNHN, measuring 57.7 x 46.0 x 41.3 mm, with 33 ribs. Ratio D= 1.27, < A= 130°; number of crenulations 27.

Description.

Shells medium to large. Shape regularly subovoid, almost equilateral but somewhat posteriorly truncated, with ribs sometimes slightly curved backwards in projection. Generally moderately elongated in adult stage (mean L/H= 0.81; range 0.73-0.89), and relatively tumid (mean W/L= 0.90; range 0.84-1.02).

Lunule, colour, hinge, rib number in agreement with general description of species. No umbonal support observed.

Rib morphology:

In PQ, thin, lamellar, homogeneous and regularly set oblique scales on top of ribs (Fig. 26).

In median and anterior parts, few and strong marginal crenulations of ribs, and lack of smoothness of ribs tops.

Material examined and distribution.

Persian gulf (see above).

Measurements of *V. assimile lacunosum*

	Height	Length	Width	L/H	W/L	ratio D	angle A	Ribs
	(mm)	(mm)	(mm)				°	
Neotype	57.7	46.0	41.3	0.80	0.90	1.27	130	33
Kuwait	58.1	44.0	43.0	0.76	0.98	1.10	130	32
Dubai	47.0	38.1	32.1	0.81	0.84	1.00	130	34
Bandar Abbas	64.0	47.0	47.8	0.73	1.02	1.21	120	35

Maximum record in literature, a height of 90 mm (Smythe, 1982).

Remarks.

The uniqueness of the subspecies *lacunosum* is the constant conjunction of two characters which can sporadically exist in the nominal subspecies:

1- Thin, lamellar, homogeneous and regularly set transverse scales on top of ribs in PQ (Fig. 26), rather than the globular, somewhat elongated variable tubercles which are generally present in the nominal subspecies (where comparable lamellar scales can also sporadically exist, Figs 7, 25).

2- Strong marginal crenulations of the ribs, and lack of smoothness of rib tops: In the median part of the shell the lateral crenulations proceed up to the top zone, forming cross-bars or partially joined rugae, all of which gives the ribs a "plaited-like structure" as Smythe says (1982: 100), figuring a good example of this special form (1982, pl. 18, fig. c). This character already appears in very young shells: in the umbonal area the crenulations of the ribs become regularly swollen very early, unlike those in the nominal subspecies. The number of crenulations is smaller: 21 to 37 crenulations (as defined above) versus 35 to 52 in the nominal subspecies.

Besides the two fundamental elements of distinction above, some other more statistical elements seem to characterize *lacunosum*. It is less elongated (average L/H= 0.81, *vs* general average= 0.77), more tumid (average W/L= 0.90, *vs* general average= 0.87), and larger (in the largest specimen H= 90 mm, as opposed to 68.8).

Vasticardium rubicundum
(Reeve 1844.)
Figs 12-14, 18-20, 27, 31.

Cardium rubicundum Reeve, 1844, Sp. 44, pl. 9, fig. 44.

Cardium mindanense Reeve, 1844, Sp. 19 [excluding the syntype figured pl. 9, fig. 19 = *Trachycardium egmontianum* Shuttle-worth, 1856, 5: 172].

Vasticardium compunctum Kira, 1959: 137, pl. 55, fig. 9.

Acrosterigma kengaluorum Voskuil & Onverwagt 1992: 33, pls 1-2.

Selected references.

Vasticardium rubicundum: Keen, 1945: 36
Cardium rubicundum: Braga, 1952: 49, pl. 10, fig. 2
NOT *Laevicardium (Trachycardium) rubicundum* Fischer-Piette, 1977: 65 [= partly *Vasticardium assimile*]
Trachycardium rubicundum: Oliver, 1992: 126, pl. 23, Figs 7a-b
Trachycardium (Vasticardium) mindanense Springsteen & Leobrera, 1986: 306, pl. 87, fig. 2

Type material.

Cardium rubicundum : Three syntypes from Zanzibar in BMNH, coll. Cuming, all larger than Reeve's figure; the largest (Figs 12-14) measures 60.0 x 49.0 x 41.3 mm.

Cardium mindanense : The name of this taxon is not to be confused with *C. mendanaense* Sowerby, 1897, which is another Indo-Pacific shell belonging to the group of *Vasticardium orbita* (see Vidal, 1997a). There are three syntypes of *Cardium mindanense* Reeve in BMNH (ex Cuming) said to have come from Mindanao (Philippines). As indicated by pencilled notes, these three specimens were initially set on the same board. They are now separated into two boxes :

- one box with the specimen figured by Reeve, subsequently erroneously labelled "holotype". Reg. N° 1978-124, measuring 41.0 x 35.2 x 29.0 mm, with 30 ribs. This shell is *Trachycardium egmontianum* Shuttleworth, 1850, from the Atlantic coast of North America. This shell was probably placed with the others by Cuming, in error, because of a certain superficial resemblance between them. Further, it was probably chosen by Reeve for the figure because it was the largest.

- a second box with two specimens of *V. rubicundum*, respective dimensions: H= 40.1 mm, 37.6 mm; L= 34.7 mm, 34.0 mm; W= 30.6 mm, 25.3 mm; the number of ribs is 36 in both specimens. These last two shells are very probably those which come from Mindanao and from which the name mindanense originates. In order to avoid possible confusion and to preserve the legitimate Indo-Pacific origin of this taxon, I have selected as lectotype *of Cardium mindanense* the largest of these (Figs 18-19); the remaining syntype, becomes the paralectotype (Fig. 20).

Acrosterigma kengaluorum: The holotype is in RMNH (56769) from Honiara, Guadalcanal Is, the Solomons, a shell measuring 30.7 x 27.8 x 21.0 mm, with 34 ribs. Twenty paratypes, all in private collections, are from the same area; their dimensions are as follows: H= 24.1 to 37.4 mm, L= 19.6 to 34.5 mm, W= 15.2 to 25.6 mm. Mean rib number 35.4 (range 32-38). Mean L/H= 0.90 (range 0.86-0.96); mean W/L= 0.75 (range 0.69-0.82).

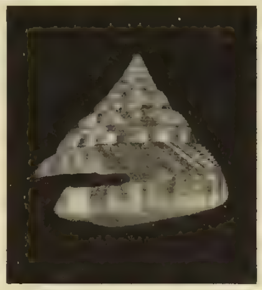
Vasticardium compunctum: This name first appears as a Kuroda M.S. name in Habe (1951: 145). Kira (1955) gives a figure and still credits the name to Kuroda M.S., but this figure is not accompanied by a description. The name is first validated by Kira (1959: 139) who gives a diagnosis of the species in Japanese, using the same figure. In 1962 (p. 156), Kira gives a description in English. The shell figured by Kira (1955 and 1959, pl. 55, fig. 9, and 1962, pl. 56, fig. 9) is considered as the holotype, with dimensions of 41.5 x 32.9 x 31.5 mm. According to a personal communication from A. Matsukuma, Kira's illustrated material is stored in Osaka City Museum (Natural History) and is not available for loan. The localities for the species given by Kira, in 1962, are the Amami and the Ryukyu Islands (Japan). Only photographs of Kira's type of *V. compunctum* have been examined but one lot in MNHN comes from the type locality, the Amami Islands, Japan.

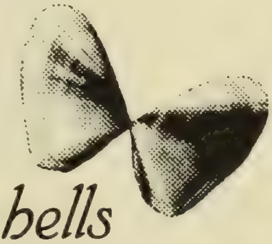
Description.

Shells regularly subovoid, almost ellipsoidal in shape and almost equilateral, except for a small truncation in posterior margin. PQ is somewhat flat or slightly depressed and forms an obtuse angle with rest of shell. Ribs generally straight, rarely slightly curved backwards in projection; adult state little elongated (mean L/H= 0.81; range 0.77-0.86) and relatively tumid (mean W/L= 0.84; range 0.78-0.84).

Exterior splashed or striped with red-purple, or sometimes brown; yellow or light orange markings can occur and predominate in specimens from southern Japan, and brown markings predominate in rest of Pacific; entirely white specimens are rare. Interior white with a colored margin and an umbonal area with two rays. Lunular area narrow, generally purple colored.

Fig. 25. *Vasticardium assimile*, left valve, specimen from Magaruque Is, Mozambique, MNHN (same as Figs 6 and 7), detail of PQ and MPQ showing particularly the ontogenic change towards the shell margin of the small posterior marginal crenulations into elongated ridges on the flank of the ribs in last ribs of MPQ; scale x 2.5. **Fig. 26.** *Vasticardium assimile lacunosum*, left valve, specimen from the Persian Gulf; detail of PQ and MPQ; scale x 2.5. **Fig. 27.** *Vasticardium rubicundum*, left valve, specimen from Zanzibar, MNHN; detail of PQ and MPQ showing particularly the additional scales in MPQ, superposed on the thin marginal crenulations; scale x 2.5. **Fig. 28.** *Vasticardium thomassini*, Holotype; detail of PQ and MPQ, scale x 4. **Fig. 29.** *Vasticardum rhegminum* left valve, same specimen as in Figs 15-17, detail of PQ and MPQ, scale x 2.5. **Fig. 30.** *Vasticardum rhegminum*, small right valve, MNHN coll. Day, detail of juvenile PQ and MPQ showing particularly in PQ the anterior edge of ribs with a thin longitudinal furrow; scale x 5.





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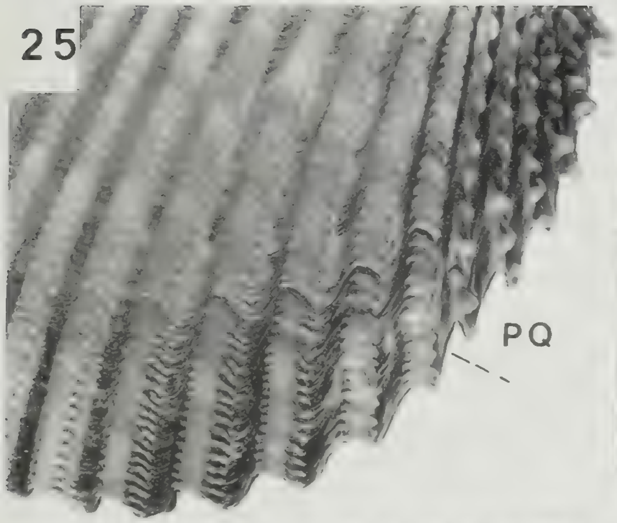

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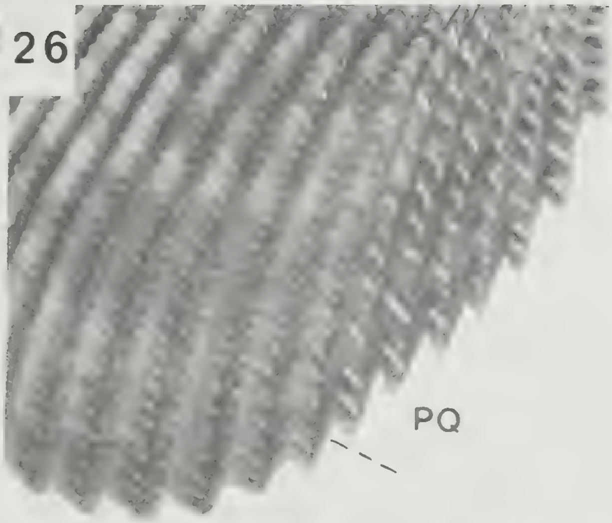

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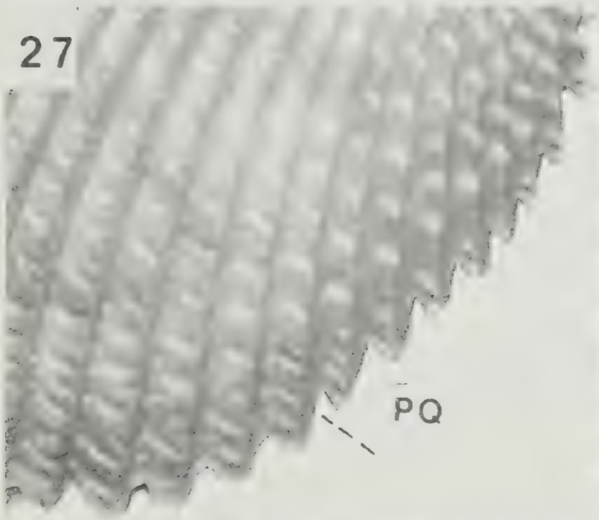

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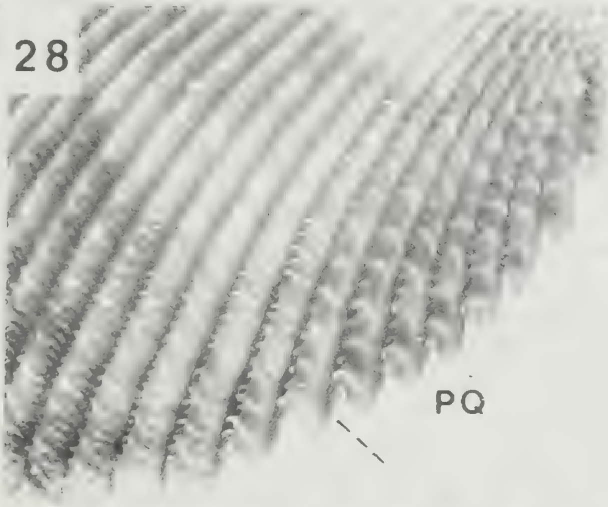

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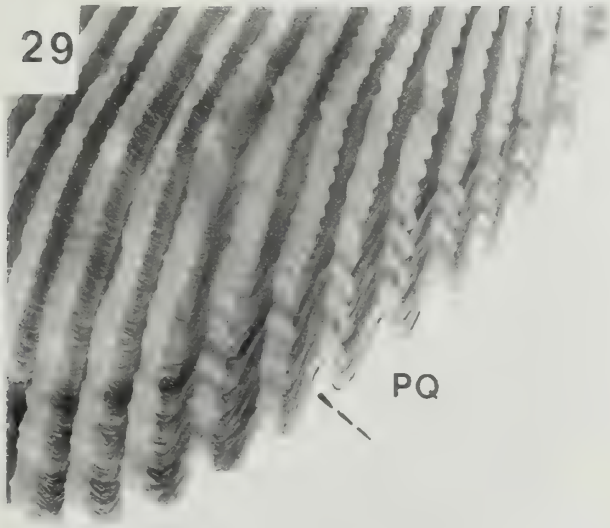

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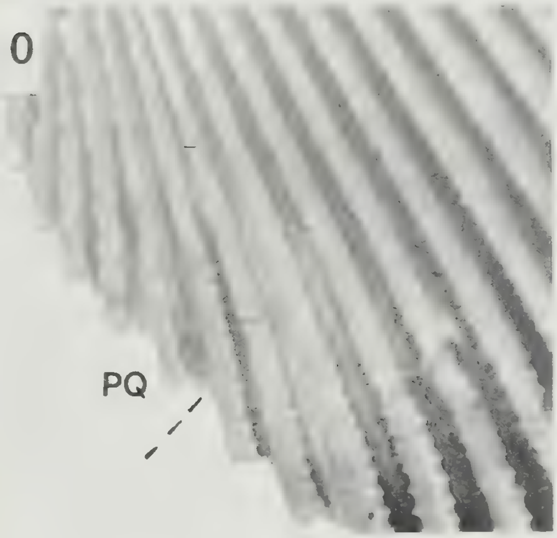


Hinge moderately arched (< A range 125-140°) and rather asymmetrical (mean ratio D= 1.15; range 1.0-1.43). Posterior cardinal in left valve (4b) rather long and high, sometimes with a sharp top; foundation of anterior laterals, mainly in right valve, moderately projecting and more hook-shaped than in *V. assimile*. No medial rib in umbonal cavity.

Mean rib number 36.0 (range 33-39).

Rib morphology:

In juvenile PQ, ribs rather low, and asymmetrical, with anterior edge overhanging interstice with a sharp continuous rib margin jutted in front of scales or rarely dividing into successive transverse bent lamellae; rib tops bear large somewhat tubercular, slightly twisted scales, obliquely set; interstices are as wide as ribs. In adult PQ, anterior edge of ribs generally becomes less sharp and often does not overhang interstices which become narrower than ribs; scales become tubercular (Fig. 27).

In juvenile median part of shell, ribs trapezoidal with rounded, narrow, almost flat tops, which are always smooth; flanks of ribs strongly ridged and furrowed, with furrows generally straight except for anterior flanks of MPQ, where they are very bent. These ornaments disappear near base of flanks, leaving a smooth basal zone. Before disappearing, these ridges thicken, forming small tubercles on their lower extremity; these tubercles, being always aligned at lower 1/3 of ribs, form regular beaded longitudinal lines along flanks of ribs; these "beads" extend into interstices, sometimes almost touching; in that latter case, the smooth inferior part of ribs and bottom of interstices form "tunnels." Bottom of interstices flat and weakly notched. Margin of top zone very variable, with respect to crenulations, from one population to another; these crenulations may or may not be present, on one or on both sides of ribs, but in anterior half of shell crenulations are always in continuity with the flank ridges which are strongly furrowed but not beaded. When these crenulations are present, flanks bear two longitudinal lines of tubercles: crenulations in the upper part, and "beads" in lower part. In adult MPQ, ribs remain or become very asymmetrical; on anterior part of ribs the finely crenulated projecting edge remains the same, but furrowing of the reduced flank lessens; in the wider posterior part, crenulations and flank furrows progressively disappear, and strong oblique straight scales develop on top and flank of rib. These scales, which are a continuation of main scales of adjacent PQ, superpose on pre-existing ornamentation and entirely replace it in the most aged part of shell (Fig. 27). In adult MAQ, and sometimes as early as in anterior part of MPQ, ribs become very asymmetrical; upper anterior part of rib flanks lowers forming a gently sloping ridged plane with the anterior part of top zone; long ridges of these planes form typical asymmetrical herringbone patterns with posterior crenulations or ridges; these herringbone-shaped ridges, first open then closed on all ribs, are often of a light color and contrast strongly with the darker color of ribs.

In juvenile AQ, flanks of ribs not beaded, interstices only finely striated by growth lines, and crenulations tend to join to form imbricated transverse ridges with a quasi-herringbone pattern. In adult AQ, these patterns evolve into imbricated continuous cross bars on top and anterior flank of ribs; tops retain a generally asymmetrical herringbone aspect.

Material examined.

Type material: Syntypes of *C. rubicundum* and *C. mindanense*, Holotype and paratype N° 1 of *A. kengaluorum*, and the following lots:

A) South Africa: East London: 1(MNHN), 1(USNM); Port Sheptone: 1(MNHN) 1(ANSP); S. Durban: 1(MNHN); N. Durban: 1(MNHN); Brighton: 1(MNHN); no specific location: 1(BMNH)

B) Mozambique: Joao Belo: 1(MNHN); Inhambane: 1(MNHN); Chidenguele: 1(MNHN); Ponta da Barra: 1(USNM)

C) Madagascar: Tulear: 5(MNHN)

D) Tanzania: Dar es Salaam: 1(AMS); Zanzibar: 4(MNHN), 1(BMNH), 2(ANSP)

E) Kenya: Shimoni: 4(BMNH)

F) Somalia: N. Mogadishu: 1(MNHN), 1(ANSP)

G) "Indian Seas": 1(MNHN)

H) Sri Lanka: no specific location: 1(MNHN,) 1(AMS)

I) Singapore: 1(AMS)

J) Indonesia-Java: Batavia Bay: 1(ZMA); Bantan: 2(USNM)

K) Indonesia-Bali: Nusa-Dua 1(LACM)

L) Philippines: Mindanao, Zamboanga: 1(MNHN); Luzon,Tabangao: 1(AMS); Luzon, Corregidor: 1(AMS)

M) Indonesia-Sulawesi: N. Paleleh: 1(RMNH)

N) Indonesia-Moluccas: no specific location: 1(ZMA)

O) Papua New Guinea: Oro Bay: 1(MNHN)

P) Japan: Amami Islands: 1(MNHN), 1(ANSP); Okinawa: 2(USNM), 1(LACM).

Fig. 31. *Vasticardium rubicundum*, left valve, specimen from Zanzibar, MNHN, detail of median part (MPQ and MAQ). Scale x 3.5. **Fig. 32.** *Vasticardium thomassini*, left valve, holotype, detail of median part (MPQ and MAQ), scale x 4.0.

Measurements of *V. rubicundum*

	Height	Length	Width	L/H	W/L	ratio D	angle A	Ribs
	(mm)	(mm)	(mm)				°	
Syntype	60.0	49.0	41.3	0.82	0.84	1.30	130o	35
Syntype	51.7	41.3	34.6	0.80	0.84	1.18	125o	37
Syntype	50.3	40.4	33.1	0.80	0.82	1.24	125o	37
Zanzibar	54.6	42.8	37.5	0.84	0.88	1.16	125o	34
Indian Seas	43.4	35.4	28.7	0.82	0.81	1.04	130o	36
Sri Lanka	40.8	33.1	26.6	0.81	0.80	1.17	135o	35
Papua N G	34.0	29.1	23.5	0.86	0.81	1.43	140o	34
Japan, Amami	46.0	35.4	33.3	0.77	0.94	1.30	130o	35

Largest specimen observed is the above syntype (H= 60.0 mm).

Distribution.

Because of the frequent confusion of *V. rubicundum* with *V. assimile*, the distribution derived from the literature is unreliable, and here only the verified localities are taken into account. Its extension into the western Indian ocean is smaller than the one of *V. assimile*, and it is not recorded from the Gulf of Aden or Arabian Sea. But *V. rubicundum* has a larger Pacific distribution, and is sporadically found as far as in Japan and the Solomons. However, it is undoubtedly locally rarer outside the southwestern zone of the Indian Ocean where it is sympatric with *V. assimile*.

Remarks.

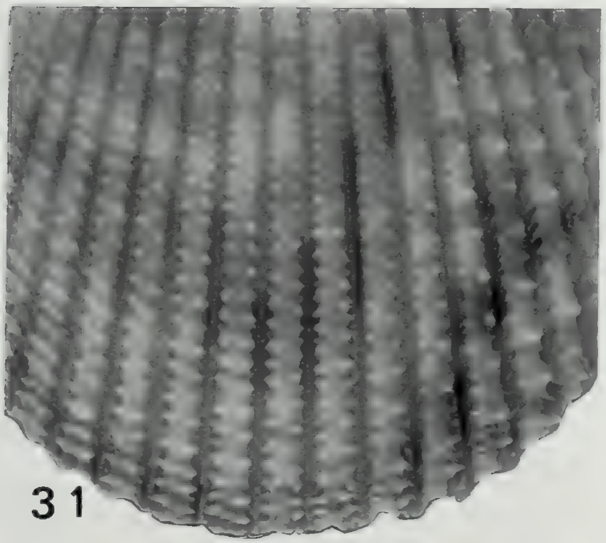
Variability of *V. rubicundum*: Unlike *V. assimile*, *V. rubicundum* is stable in shape and rib ornamentation. The only variable element is color. The specimens from the southwestern Indian Ocean are rather colored with purple or pink (like *V. assimile*). In the westernmost Pacific, the colors are rather brown, and in Japan they are entirely yellow to light orange, sometimes almost white. Two specimens from Singapore, in AMS, are entirely white.

Differences from *V. assimile*: Three easily observed main characters of *V. rubicundum*, among others, separate it from *V. assimile*:

1) Beaded structure of the ribs in the young specimens; flanks of ribs are smooth in *V. assimile*.

2) Large oblique scales on top of ribs in MPQ in adult specimens; tops smooth in v. assimile (compare Fig. 25 and Fig. 27).

3) Strongly marked asymmetrical herringbone patterns on the ribs in the median and anterior parts of the shells in adult specimens (no herringbone in *V. assimile*).



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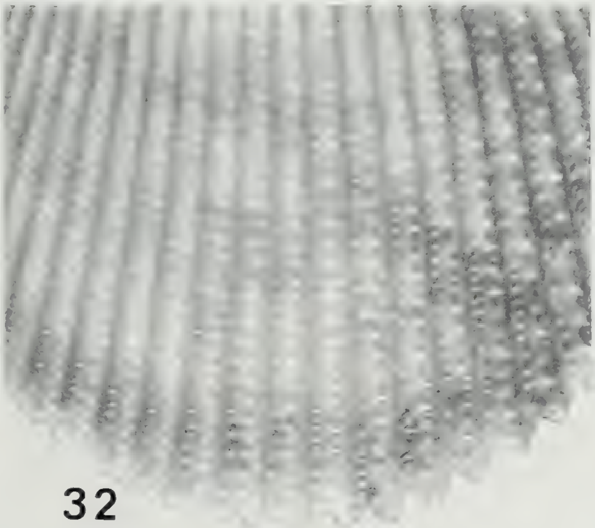

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Differences from *V. vertebratum*: A beaded double ornamentation readily comparable to the one in *V. rubicundum* also exists in the *Australian V. vertebratum* (Jonas, 1844) [*V. reeveanum* (Dunker, 1852)], which is also of a comparable reddish color. However this species belongs to the species-group of *V. flavum* (Linné) (see VIDAL 1997b) and significant characters separate the two shells. *V. vertebratum* is characterized by

1) Average number of ribs: 29, instead of 36

2) Juvenile ribs in PQ rather symmetrical, without any anterior sharp edge, but with secondary ornaments (small scales and ridges, in addition to the main scales, on the margins of top).

3) Ribs always rather symmetrical.

4) Interstices much more strongly striated.

5) Double beaded ornamentation regular and constant, not limited to the young parts of the shell.

6) Herringbone pattern on the ribs rare.

Vasticardium rhegminum

(Oliver & Chesney, 1997).

Figs 15-17, 29-30

Acrosterigma n. sp. (b) Oliver, 1995: 246, fig. 1092.

Trachycardium (Acrosterigma) rhegminum Oliver & Chesney, 1997: 69, Figs 39-42.

Type material.

Five immature bivalved shells, live collected from off Ras Madrakah, Gulf of Masirah, Oman, coll. "John Murray" Expedition Sta. 53, 19°22'36"N-57°53'00"E, 13.5 m. Holotype in BMNH. Four paratypes, three in BMNH, one in NMW reg. NMW.Z.1994.

Description.

Shell medium-sized , solid, and rather heavy, nearly equilateral, and only very slightly oblique (ribs only slightly curved backwards in projection). Outline ovate, generally elongated (mean L/H= 0.83; range 0.77-0.87) and moderately tumid (mean W/L= 0.84; range 0.80-0.90). Anterior dorsal slope longer and steeper than posterior, and posterior margin slightly straightened. Lunular area small, elongate and purple colored.

External color white to beige with an irregular pattern of pink (generally dominant) to light purple-brown; internally, margin tinged orange-pink along posterior edge and lightly suffused pink or orange-pink over umbonal cavity, with two umbonal rays.

Hinge wide and strong in adult shells, markedly acutely angled compared to other species of group (< A range 105-115°) and of different asymmetry (ratio D about 0.95). Foundation of anterior laterals not hook-shaped, and a long, elevated medial rib (umbonal support) occurs in umbonal cavity of all shells.

Mean rib number 40.2, range 38-43.

Rib morphology:

In juvenile PQ, initial rib morphology conforms that of other species of this group: ribs asymmetrical, with anterior edge overhanging interstice, and a sharp continuous margin jutted in front of scales; rib tops bear large somewhat tubercular, slightly twisted scales obliquely set; interstices are as wide as ribs. In adult PQ, scales flatten with growth, become round and widen, occupying all the top area, and forming successive oblique "waves", touching one another; these waves form crenulations on posterior margin of ribs, but on anterior margin they gradually disappear, forming a straight line which progressively overhangs interstice above original rib margin (Fig. 29). This results, on anterior margin, in a double overhanging edge divided by a well delineated thin furrow (Fig. 30).

In juvenile median part of shell, high ribs with roundly triangular top zones and crenulated margins overhang smooth and flat-bottomed interstices; flanks smooth, not separated from interstices. In adults (Fig. 29), ribs become very high, and progressively asymmetrical, with vertical smooth flanks, and smooth flat tops with more or less regularly crenulated margins overhanging interstices. Interstices deep, with flat, smooth bottoms, as wide as or wider than ribs.

In AQ, and as early as in anterior part of MAQ in very adult shells, marginal crenulations join from one side to other of rib tops, forming transverse oblique ridges, rarely with a herringbone pattern.

Material examined.

In addition to the type specimens, the following lots:

A) 43 valves, as type series, BMNH.

B) 15 valves, from storm beach opposite the British Eastern Relay Station camp, Masirah Island, in NMW coll. Oliver & Chesney Nov 1992 Reg. NMWZ.1993.X.Z.

C) 1 valve from Masirah area, in BMNH coll. Biggs 1967.

D) 3 small valves from Masirah Island, in MNHN coll. Day 1994.

E) 4 valves from Masirah Island, in MNHN coll. Fuller 1968

F) 1 bivalved specimen from Masirah area, in MNHN leg Sue Hobbs 1995 (Figs 15-17).

G) 1 bivalved specimen from Masirah area, in Sue Hobbs' private coll.

Measurements of *V. rhegminum*

	Height	Length	Width	L/H	W/L	ratio D	angle A	Ribs
	(mm)	(mm)	(mm)				°	
Holotype	34.7	28.9	24.4	0.84	0.84			38
MNHN (Hobbs)	53.6	39.4	36.4	0.73	0.92	0.94	105	39
Hobbs coll.	52.0	38.9	34.5	0.75	0.89	0.95	105	41
MNHN (Fuller)	63.5	46.9	(42.0)	0.74	0.90		110	42
MNHN (Fuller)	45.0	34.6	(32.4)	0.77	0.94		115	39
MNHN (Fuller)	27.0	22.6	(20.0)	0.84	0.88	1.00		38

Largest specimen observed, the above right valve from Masirah Island, in MNHN coll. Fuller (H= 63.4 mm).

Distribution.

To date, this species is known only from the Bay of Khalij (Masirah), on the southern coast of Oman, where it is sympatric with *V. assimile*.

Remarks.

Variability of *V. rhegminum*: This species is remarquably constant from one specimen to another, in all growth stages.

Differences from the three other species of the group: The average rib number of *V. rhegminum* is higher than in *V. assimile* and *V. rubicundum* (40.2 *vs* 33.4 and 35.6). This species differs also from the three other species of the species group by its very much smaller angle A, its characteristic "wavy" posterior zone with a furrowed anterior edge, and also by its very high regular ribs with smooth flanks and wide smooth interstices in the other parts of the shell.

Differences from some other species of *Vasticardium* with high ribs and wide interstices: The very special character of PQ is sufficient to separate *V. rhegminum* from several other forms which also have very high ribs and wide interstices, such as some subspecies of *V. elongatum* (see VIDAL 1993), *V. fidele* (see VIDAL 1992), and some subspecies of *V. orbita* (see VIDAL 1997a).

Vasticardium thomassini sp. nov.

Figs 21-24, 28, 32.

Type material.

Holotype (Figs 21-24, 28, 32), a shell from Tulear area (Madagascar), Thomassin's sta. D21, 43°49'E-23°31'S, 45m, in MNHN. Paratype 1, a left valve from the same station, in MNHN. Paratype 2, a left valve from Tulear area, Thomassin's sta. 211, 43°37'E-23°31'S, 12m, in MNHN. Paratype 3, a shell from south side of Pwakun Is, W.Zanzibar, ca. 25 m, in ANSP 213809. Paratype 4, a right valve from between Port Shepstone and Port Edward, Natal (South Africa), in MNHN, leg Lavranos ex Polak.

Description.

Shell small to medium, regularly subovoid, almost ellipsoidal in shape an almost equilateral, except for a small truncation in PQ; holotype has also a small truncation in MPQ. Ribs generally straight, rarely slightly curved in projection. Adult shell little elongated (L/H range in the three largest shells 0.81-0.83) and relatively tumid (W/L range in the same shells 0.82-0.87). Lunular area well delineated, rather narrow, dark purple colored.

Exterior splashed with yellow to orange, with darker irregular stripes; interior white with an umbonal area yellow to orange, sometimes with two darker rays; margin not colored.

Hinge moderately arched (<A circa 135°) and almost symmetrical (ratio D circa 1.0 or a little more). Posterior cardinal in left valve (4b) rather long and high, with a pointed top. Foundation of anterior lateral in right valve moderately hook-shaped. No medial ridge in umbonal cavity.

Rib number ranges 42-45.

Rib morphology:

In juvenile PQ, ribs rather low and assymetrical with anterior edge overhanging interstice with a sharp continuous margin jutted in front of scales or dividing into successive transverse bent lamellae; rib tops bear large, somewhat tubercular, slightly twisted scales, obliquely set. Except for the two last ones, interstices are narrow. In adult PQ (Fig. 28), anterior edge of ribs becomes less sharp and does not overhang interstice: the previous thin bent lamellae of anterior edge become small flank scales with a different obliquity from the one of the main scales, forming an angle with them, and being about twice more numerous.

In juvenile median part of shell, ribs are, at first, flatly rounded, smooth, with progressive appearance of small serrations at their lower part, separated from interstice which is finely striated or notched. Then basal serrations enlarge, become overhanging and ribs progressively become roundly triangular. In adult MPQ (Fig. 28), ribs remain about same as in PQ with same assymmetry (anterior flank shorter and steeper), but posterior flank becomes finely ridged, when anterior small scales become more numerous and progressively change, onwards, into small, thin flank ridges; the equivalent of PQ main scales change into tubercles on top of ribs. In adult middle of shell (anterior part of MPQ and posterior part of MAQ, Fig. 32), ribs become about symmetrical and triangular, with both flanks bearing numerous thin ridges not reaching interstice, shorter and more numerous in anterior flank, forming an herringbone pattern with the posterior ones. Top zone progressively loses, onwards, its tubercles and becomes smooth.

In AQ, ribs become more asymmetrical (posterior flank shorter) and slightly overhanging and lateral ridges progressively join together to form top imbricated rugae.

Material examined and distribution.

The type series, consisting only of 1 valve from S. Natal, 1 specimen and 2 valves from S.W. Madagascar, 1 specimen from Zanzibar. In these three localities it is sympatric with *V. assimile* and *V. rubicundum*.

Measurements of *V. thomassini*

	Height	Length	Width	L/H	W/L	ratio D	angle A	Ribs
	(mm)	(mm)	(mm)				°	
Holotype	34.0	27.7	23.5	0.81	0.85	0.95	130	43
Paratype1	28.2	23.4	(20.4)	0.83	0.87	1.0		42
Paratype2	32.7	26.7	(22.0)	0.82	0.82	1.0		44
Paratype3	23.0	20.2	15.4	0.88	0.76	1.10	135	45
Paratype4	18.5	16.1	12.0	0.93	0.75		135	44

Etymology.

Bernard A. Thomassin conducted extensive field work in Tulear area (S.W. coast of Madagascar), between 1963 and 1972, for ecological studies (see THOMASSIN, 1978).

Remarks.

Differences from *V. rubicundum*: *V. thomassini* is very close to *V. rubicundum* as far as shape, morphometric data, lunule, hinge are concerned; it differs from the specimens from Africa in absence of purple coloring in the exterior, and is closer, in that domain, to the yellow-orange forms of Japan (*compunctum*). It differs from all the forms of *V. rubicundum* in:

(1) Number of ribs ranging 42-45, when the maximum in *V. rubicundum* is 39.

(2) Rib morphology (compare Figs 28 and 32 with Figs 27 and 31): presence in *V. thomassini* of secondary anterior small scales in PQ and much more numerous lateral serrations or ridges in the rest of the shell; in *V. thomassini* the interstices in the median part of the shell are much narrower (see Fig. 32); in this median part, the small lateral ridges are much more numerous and form a better herringbone pattern in *V. thomassini*; absence also of the "double-beading" of the ribs in the median part of the juvenile shell which characterizes *V. rubicundum*.

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Description of *Trophon iarae* n.sp., a new muricid from southern West Atlantic (Gastropoda: Muricidae) with illustration of related species

Roland HOUART
Research Associate, Institut royal des Sciences naturelles de Belgique
Département des Invertébrés Récents
Rue Vautier, 29, B-1000 Bruxelles, Belgium

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ABSTRACT. *Trophon iarae* n.sp. is described and compared with *T. plicatus* (Lightfoot, 1786), *T. acanthodes* Watson, 1883, *T. varians* (d'Orbigny, 1841), and *T. geversianus* (Pallas, 1774).

INTRODUCTION

Some time ago, I received from Pedro H. Kahvedjian, a shell collected off Uruguay. After comparison with specimens in my collection, I identified it as a form of *Trophon plicatus* (Lightfoot, 1786). Recently, Prof. Emily Vokes asked if I would agree to study, and eventually to describe a *Trophon* sp. from Brazil. The specimen was sent to her by Prof. E. Rios, but because of time constraints, she delayed its study. I accepted of course, always being very excited by new, and unusual material.

The specimen I received is gorgeous, and at first sight, I also felt it was undescribed. Moreover, when comparing it with my reference material, I came back to the unusual form of *T. plicatus* from Uruguay, and immediately I saw that it was the same species. The specimen from Uruguay is smaller, somewhat damaged, and dead taken. However, now, with the help of the new material, it is possible to separate it definitively from the other Magellanic species of *Trophon*.

Another specimen of *T. iarae* n.sp. was illustrated by CERNOHORSKY (1977: 117, fig. 18), as *T. plicatus*, from the Falkland Islands.

The radula of the Brazilian specimen was illustrated by CALVO (1987: 136, fig. 99), and wrongly identified (as I initially did), as *T. plicatus*. However, in her table of dimensions, CALVO (1987: 174), cites that specimen as C = 50 mm, L = 35 mm (C = comprimento = length; L = largura = width). This does not agree with the dimensions of the shell. Nevertheless, it was confirmed by Prof. Rios that the radula illustrated by Calvo was extracted by her from that shell, so that I conclude the dimensions given by Calvo were probably erroneously taken from another shell.

SYSTEMATIC ACCOUNT

Genus *Trophon* Montfort, 1810

Type species by original designation: *Murex magellanicus* Gmelin, 1791 (= *Buccinum geversianum* Pallas, 1774); Recent, Magellanic region.

Trophon iarae n.sp.
Figs 1-5

Type material.

Holotype n° 6731, Museu Oceanográfico "Prof. Eliézer de C. Rios", 74.6 X 61 mm; 1 paratype coll. R. Houart, 53.8 X 39.4 mm.

Type locality.

Off Albardão, RS, Brazil, collected by fishing boat "Pescal 2", C. Pontes, 1961, in 55 m.

Other localities.

Off Uruguay, by fishermen (paratype R. Houart); East of Lively Id, E Falkland Islands, in 79 m (CERNOHORSKY, 1979).

Distribution.

From the Falklands Islands to Albardão, RS, Brazil, living in 55-79 m.

Description.

Shell large sized, up to 74.6 mm in length at maturity (holotype), heavy, strongly lamellate. Spire moderately high, up to 6, broad, strongly shouldered, teleoconch whorls. Suture adpressed. Protoconch unknown (broken).

Axial sculpture of teleoconch whorls consisting of strongly raised, thin lamellae, more strongly developed on shoulder, producing long, narrow, spinelike projections. First whorl with 8 lamellae, second to fourth with 8 or 9, penultimate with 10, last whorl with 13 lamellae. Other axial sculpture of numerous, fine, narrow, growth striae. Spiral sculpture consisting of a single carinal cord, forming long, spinelike expansions at intersection with axial lamellae.

Aperture moderately large, broad, roundly-ovate. Columellar lip smooth, lip partially erect, adherent at adapical extremity. Outer lip weakly erect, smooth. Siphonal canal moderately short, narrow, straight, open.

Shell entirely white.

Operculum dark brown, roundly-ovate, with terminal nucleus in lower right.

Radula (in CALVO, 1987: fig. 99): Rachidian with long central cusp; lateral cusps long with small, inner lateral denticle; marginal area with several small denticles or plicae; marginal cusps short.

Discussion.

From *Trophon plicatus* (Lightfoot, 1786) (Figs 8-10), *T. iarae* n.sp. differs in having a higher spire, and in having long, almost horizontal, narrow, carinal, open spines, while the axial lamellae in *T. plicatus* end as short to very short, mostly adapically bent, broad, open expansions. The shoulder (or sutural ramp) is broad, weakly convex, and abapically sloped in *T. iarae*, but almost horizontal and narrow in *T. plicatus*. The siphonal canal is narrower and longer relative to the shell length in *T. iarae*. *Trophon acanthodes* Watson, 1883 (Figs 6-7) also has a broad, weakly convex, sloped sutural ramp, and narrow, open, carinal spines as in *T. iarae*, but *T. iarae* differs in other aspects. The siphonal canal of *T. iarae* is twice as short, for a shell with a same number and same length of spire whorls; the axial lamellae are more obvious and broader compared to those of *T. acanthodes* which are low, or almost obsolete; the spiral sculpture is absent in *T. iarae*, while consisting of narrow, conspicuous, rounded cords in *T. acanthodes*.

The two other Magellanic species, namely *T. varians* (d'Orbigny, 1841) (Fig. 12), and *T. geversianus* (Pallas, 1774) (Fig. 11) differ in many aspects: *T. varians* has a rounded shell, smooth, almost smooth, or ornamented with coarsely woven spiral cords, without lamellae. *T. geversianus* has more or less, strong, obvious, spiral sculpture, and usually more numerous, lower, axial lamellae. *T. geversianus* also have a broader aperture. Both species have a shorter, broader, siphonal canal.

The operculum of *T. iarae* n.sp., *T. plicatus*, *T. geversianus*, and *T. varians* all have a similar morphology. The radula is also almost identical in *T. iarae*, *T. geversianus*, and *T. varians*, however, it is quite different in *T. plicatus*, in having broad, serrate, lateral cusps (POWELL, 1951; VOKES, 1992).

Trophon acanthodes is also different in having a narrower, triangular operculum with terminal nucleus, and a broader radula with a shorter, narrower, and more prominent central tooth.

Etymology.

Named after Iara Swoboda Calvo, oceanographer in Museu Oceanográfico "Prof. Eliézer de C. Rios", who extracted and illustrated the radula of the holotype.

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Figs 1-3. *Trophon iarae* n.sp. Off Albardão, RS, Brazil, 55 m, Museu Oceanográfico "Prof. Eliézer de C. Rios", 74.6 x 61 mm (whitened, photographs E. VOKES), holotype n° 6731 (siphonal canal damaged after the photograph was taken). **Fig. 4.** Distribution of *Trophon iarae* n.sp.

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Fig. 5. *T. iarae* n.sp. Off Uruguay, 54 mm, paratype coll. R. Houart. **Figs 6-7.** *T. acanthodes* Watson, 1883. Off Argentina, 59° S, 38° W, 86 mm, coll. R. Houart. **Figs 8-9.** *T. plicatus* (Lightfoot, 1786). Rocha, Uruguay, 63.4 mm, coll. R. Houart. **Fig. 10.** *T. plicatus* (Lightfoot, 1786). Rocha, Uruguay, 34.4 mm, coll. R. Houart. **Fig. 11.** *T. geversianus* (Pallas, 1774). Straits of Magellan, 93 mm, IRSNB IG 10591. **Fig. 12.** *T. varians* (d'Orbigny, 1841). Patagonia, 76 mm, syntype MNHN.

Oliva ouini, a new species from Hansa Bay, Papua New Guinea, with notes on the anatomy of *O. oliva* (L., 1758) [1]

Yuri KANTOR
A. N. Severtzov Institute of Problems of Evolution,
Lenin Avenue 33, Moscow 117071, Russia.
and
Bernard TURSCH
Laboratoire de Bio-Ecologie, Faculté des Sciences, Université Libre de Bruxelles,
50 av. F.D. Roosevelt, 1050 Brussels, Belgium.

KEYWORDS. Olividae, *Oliva ouini*, sp.nov., *Oliva oliva*, anatomy, shell morphometry.

ABSTRACT. *Oliva ouini*, sp. nov. from the Western Pacific Ocean is described and compared to its closest relative: *O. oliva* (L., 1758). The shells of the two species differ by several characters and are completely separable in scatter diagrams. The anatomy of the two species is described and shown to differ for several features.

RESUME. *Oliva ouini*, sp. nov. de l' Ouest de l'Océan Pacifique est décrite et comparée à l'espèce la plus proche: *O. oliva* (L., 1758). Les coquilles des deux espèces diffèrent par plusieurs caractères et sont complètement séparables en diagrammes bivariés. L' anatomie des deux espèces est décrite; elle diffère par plusieurs points.

INTRODUCTION.

Since 1973, the various biotopes of Hansa Bay (Papua New Guinea) have been systematically and repeatedly explored for their *Oliva* fauna. The first specimens of the small species described below were found in May 1992, by SCUBA diving in depths of 6-7 m, around the bow of a small World War II Japanese wreck locally known as the "*Small Awar wreck*". When sifting the sediment with a small hand dredge (mesh: 8 mm), Mr. Jean-Marc OUIN (then Manager of Laing Island Biological Station) noticed that some small, dark *Oliva* were escaping through the mesh. These specimens were unusually fast and agile, re-burying very rapidly in the sediment, in which –being highly cryptic– they vanished if not caught immediately. Albeit quite elusive, the species is not rare around the wreck and, during subsequent years, a total of over 30 specimens has been observed.

The discoverer immediately suggested it was a new species. One of us (BT) was long hesitant because the shells somewhat resemble juveniles of the highly variable *Oliva oliva* (L., 1758), especially the Melanesian variety *longispira* Bridgman, 1906, also present in Hansa Bay. The new form was recognizable at first sight, but so are many local forms of *O. oliva*, a species known to exhibit extreme inter-population differences even within short distances (see TURSCH 1994). The protoconchs are quite similar. The possibility of dealing with an unusual, isolated population of *O. oliva* was increased by the fact that all specimens known at the time were not syntopic with *O. oliva* and came from an area of less than 200 square meters (this objection can now be discarded: the species has recently been found in Vanuatu). So the status of the new species remained long undecided [it was reported as "*species ZHB*" in a study of the *Oliva* of Hansa Bay (VAN OSSELAER *et al.* 1993)].

Although *O. ouini* is easily separated from *O. oliva* (L., 1758) by morphometric analysis of the shell (see below) and lives in another habitat (at least in Hansa Bay), it was felt that study of the soft parts could provide independent evidence of distinct specific status. This would also provide an opportunity of describing the hitherto unknown anatomy of *Oliva oliva* (L., 1758), the type species of the genus *Oliva*. The anatomy of *Oliva* species has indeed been quite neglected so far, excepted for the works of KÜTTLER (1913), MARCUS & MARCUS (1959) and KANTOR (1991).

Family OLIVIDAE Latreille, 1825
Subfamily OLIVINAE Latreille, 1825
Genus *Oliva* Bruguière, 1789.
Oliva oliva (L., 1758).

SHELL.

The shell of *O. oliva* is extremely variable, with the consequence that at least two different species form an "*O. oliva* complex" and are usually confused by authors. Their distinction by morphometric analysis and their geographical distribution have been treated in

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[1] This is paper 30 in the series *Studies on Olividae* and Contribution n° 350 from Laing Island Biological Station.

TURSCH, MISSA & BOUILLON (1992). *O. oliva* presents a very large inter-population variation: many populations (even within very short distances) can be easily separated, although the whole set of populations forms one unbroken morphological continuum (see TURSCH 1994). The variability of *O. oliva* is further increased by non isometric growth: the shape of the shell varies with age (see TURSCH 1997). The distribution of shell sizes within one population is very uneven and has been shown to remain constant throughout the year (see TURSCH, OUIN & BOUILLON 1995).

ANATOMY.

17 specimens within the shell length range (H) 11.6-33.4 mm were examined (Table 3). The radulae of 5 specimens were studied by scanning electron microscopy (SEM).

External anatomy. The body of a specimen with H: 15.8 mm consists of 3.75 postnuclear whorls (Pl. 3, Figs. A-B), the mantle cavity spanning *ca.* 1/3 whorl. In alcohol-preserved specimens, the body is pale yellowish, unpigmented. The foot is thin, folding longitudinally during fixation; posteriorly it forms a pouch (Pl. 3, Fig. A - fp). The length of the columellar muscle varies from 1 whorl (specimen H: 15.8 mm) to 1.5 whorls (specimen H: 33.4 mm).

Mantle cavity. Mantle edge even. Mantle rather thick, although the osphradium and the ctenidium are seen through it. Siphon long with smooth edges, extending substantially [33% to 44% L (lip length)] beyond the mantle edge.

Osphradium yellowish, bipectinate, becoming relatively smaller as the animal grows (compare Pl. 3, Fig. D and Pl. 4, Fig. D). It varies from 83% (specimen H: 13.1 mm) to 22% (specimen H: 33.4 mm) of the width and from 84% (specimen H: 12.3 mm) to 62% (specimen H: 33.4 mm) of the length of the large, deeply hanging ctenidium. Osphradium asymmetrical: there are more lamellae on its right side than on the left (Table 3); the total number of lamellae increases as the animal grows. The ctenidium occupies nearly 4/5 of the mantle length. The ctenidium becomes wider and the lamellae become relatively fewer as the molluscs grows (compare Pl. 4, Figs. E and F). Hypobranchial gland moderately glandular, forming very low transverse folds. Anterior mantle tentacle flat, usually much shorter than the siphon. Posterior mantle tentacle not pigmented, short and measuring 15% to 25% of H. Mantle lobe small, concave.

Digestive system. One specimen (male, H 15.8 mm) was preserved with its proboscis everted (Pl. 3, Fig. E). The proboscis is not long (11% of H when contracted to 28% of H when extended), narrow (length/diameter ~ 4.3-8) and lies within the thin-walled proboscis sheath. The proboscis can be highly retracted during invertion, so that the buccal mass (Pl. 5, Fig. E - od) and the radular sac (rs) protrude beyond its posterior end.

Several thin retractor muscles are attached to the middle part of the rhynchodaem (wall of the proboscis sheath) when the proboscis is retracted (Pl. 5, Fig. E - prr). During evertion of the proboscis, the entire length of the rhynchodaem becomes the proboscis walls and the point of attachment of the retractors shifts inside the proboscis.

After the proboscis, the oesophagus is rather narrow and forms a long loop when the proboscis is inverted. During evertion, the loop is completely straightened.

Valve of Leiblein small and poorly delimited from the oesophagus (Pl. 3, Fig. E - vL; Pl. 5, Fig. E), which becomes very narrow to pass through the nerve ring. The nerve ring is large, massive and without visible borders of ganglia (Pl. 3, Fig. E - nr; Pl. 5, Fig. E).

After the opening of the duct of the gland of Leiblein, the posterior oesophagus widens markedly towards the stomach (Pl. 3, Fig. E; Pl. 5, Fig. E - poe).

Gland of Leiblein medium-sized, tubular, coiled, very light-brownish, opens into the oesophagus by a constricted duct which is close to the nerve ring (Pl. 5, Fig. E - dgL) or lies separately on the right side of the foregut (Pl. 3, Fig. E). Salivary glands medium-sized, ramified-tubular, rounded or elongated. Salivary ducts rather thick; shortly after leaving the glands (anteriorly to the valve of Leiblein) they enter the oesophagus walls and pass inside them.

The unpaired small accessory salivary gland is partially embedded in the right salivary gland (Pl. 3, Fig. E; Pl. 5, Fig. E - asg), with a thick duct (dasg) which passes at the right side of the oesophagus.

The radula consists of 132 (specimen H: 12.3 mm) to 184 (specimen H: 23.0 mm) rows of teeth, of which 25-42 rows are not yet completely chitinized. Radula width varies from 0.73% to 1.30% of H (mean: 0.93%; σ: 0.21; *n*=9). The lateral teeth are of complex shape, typical for the genus *Oliva*: subtriangular, slightly concave plates with narrow base and curved hook-like tips. The basal part of the rachidian teeth has distinct borders; in dorsal view the anterior (directed towards the mouth) edge is clearly convex, semi-elliptical. The rachidian tooth has 3 cusps, the central one being the smallest. In young specimens the cusps are very close to each other (Pl. 8, Figs. 1-3); in larger specimens their spacing slightly increases (Pl. 8, Fig. 4).

The radulae of specimens from two populations in Hansa Bay have been compared: Boro Beach (steep white beach, strong wave action) and Sisimangum Beach (gently sloping black beach, moderate wave action). The two populations are separated by less than one kilometer but their shells are very different: on Sisimangum Beach most specimens are very dark, with short spires while on Boro Beach all specimens are whitish with long spires (see TURSCH 1994). The studied specimens of the Boro Beach population (Pl. 8, Figs. 5-8) appear at first glance to have broader rachidian teeth. This illusion stems from a change in general tooth shape (it is relatively shorter) but the ratio of width to H of the rachidian teeth is practically the same as in the specimens of the Sisimangum population. In the Boro Beach specimens this ratio is 0. 27-0. 33%, while in Sisimangum specimens it is 0.23-

0.31%. The rachidian teeth of the Boro Beach specimens have more widely spaced cusps and present minute serrations between the cusps (Pl. 8, Figs. 7-8). For the moment we do not know if this is an ontogenetic change because we have no young specimens from Boro Beach (where collecting conditions are rough).

Stomach small; its size and shape differ greatly among individuals and probably depend on physiological conditions. The stomach has a rather long caecum and a digestive gland with a single duct, which opens just at the entrance of the oesophagus (Pl. 4, Fig. C; Pl. 5, Fig. F) (the entrance of the oesophagus is not clearly seen on Pl. 4, Fig. C). The stomach has a small posterior sorting area and well pronounced typhlosoles. Anterior sorting area not defined.

Rectal gland absent.

Reproductive system. The gonad, together with the digestive gland, occupies the upper whorls of the visceral mass, starting at the level of the nephridium. The gonad is usually overlaid by the digestive gland and is sometimes not seen from the outside (Pl. 5, Figs. A, D). Penis in mature males is large, simple, terminating in more or less long prong (Pl. 5, Fig. G) which is absent in immature males (Pl. 5, Fig. H). Accelerated growth of the penis probably occurs at a shell length of about 14 mm. A male with H: 13.1 mm still had a penis 0.08 mm long (penis length 0.6% H), while male with H: 14.1 mm already had a penis 6.25 mm long (penis length 44% of H), although not fully formed (Pl. 5, Fig. H). Afterwards, the relative length of the penis remains more or less the same throughout life, or even can become relatively shorter (penis length 34% of H in specimen with H: 25.8 mm; 41% of H in specimen with H: 27.0 mm). The shape changes (appearance of the prong) and the seminal duct become well distinct and visible through the penis walls (Pl. 5, Fig. G). Some males with H: 16.0 mm may still remain immature.

The maturation of the females occurs probably at the same shell size. The smallest mature female seen by us was H: 16.2 mm. It can thus be concluded that *O. oliva* reaches sexual maturity at a shell length of at least 15 mm.

Ontogenetic changes. Besides sexual maturation, the only significant ontogenetic change noticed by us is the relative size of the osphradium and the ctenidium. In young specimens the osphradium has nearly the same size as the ctenidium; it becomes much smaller in grown-up specimens.

Oliva ouini sp. nov.

"*Oliva* sp. ZHB"; Van Osselaer *& al.* 1994: 30.

Type Material.

Holotype (H: 15.62 mm; D: 5.91 mm): Natural History Museum, London [BM(NH)] (Pl. 1, fig. 1).

Paratype 1 (H: 13.50 mm; D: 5.51 mm): Institut Royal des Sciences Naturelles de Belgique, Brussels (I.R.N.S.B.) (Pl. 1, Fig. 2).

Paratype 2 (H: 13.59 mm; D: 5.57 mm): Zoological Museum, Moscow State University (ZMM) n°.Lc 23326 (Pl. 1, fig. 3).

Paratype 3 (H: 13.66 mm; D: 5.64 mm): United States National Museum, Smithsonian Institution (USNM) (Pl. 1, fig. 4).

Paratype 4 (H: 12.91 mm; D: 5.04 mm): Muséum National d'Histoire Naturelle, Paris (MNHN) (Pl. 1, fig. 5).

Paratype 5 (H: 12.05 mm; D: 4.97 mm): Australian Museum, Sydney (Pl. 1, Fig. 6).

Type locality. Hansa Bay, Papua New Guinea (4°10'30" S - 144°52'47" E). Near bow of "Small Awar Wreck", grey sand, 6-7 m.

SHELL.

SIZE: up to about 17 mm.

GENERAL SHAPE: biconical, elongated.

SPIRE: conical, elevated.

PROTOCONCH: greyish-white to dark purplish-grey. Nuclear whorls: mean 3.6. Lower part of last nuclear whorl purple. Transition to teleoconch straight, well defined.

SPIRE WHORLS: profile flat. First postnuclear whorl white. Subsequent whorls with long axial stripes.

FILAMENT CHANNEL: rather narrow, deep, black.

BODY WHORL:

SHELL BACKGROUND: yellowish-cream to whitish.

COLOUR PATTERN: Fine to very fine pattern of brown zigzags, in many cases coalescing into nearly solid brown zones. The shell background is then seen mostly in triangular zones, often coalescing into axial series and commonly delineated with a darker brown line. The zigzag pattern is reinforced by darker chevrons, frequently arranged into axial series. In addition, most specimens have bold dark brown axial lines, following growth lines.

SUBCHANNEL PATTERN: long, dark radial strokes, fainting adapically and often coalescing into a continuous line.

COLUMELLA: somewhat translucent, light purplish grey to flesh, white in faded specimens. 8 to 9 (generally 8) very strong oblique, parallel columellar plications forming regular, rounded columellar teeth.

FASCIOLE: whitish-grey with dark-brown spot at tip.

SUPRAFASCIOLAR BAND: dark grey, patterned with coarse, curved, dark lines in its lower zone, sometimes extending in the upper zone.

APERTURE: chocolate-brown. Inner margin of lip darker. Edge of lip beige. External contour of lip slightly angulate (bulging) near adapical third of aperture. The elongated aperture is rather distant from the filament channel of the previous whorl.

Quantitative data. The meaning of the measurements used in this work is sketched in Figs. 1 and 2. The linear teleoconch measurements H, L, D and LW, the number of nuclear volutions NW and the number of post-nuclear volutions PNW were defined in TURSCH & GERMAIN (1985); the linear protoconch measurement RES5 was defined in TURSCH &

GERMAIN (1986); the linear protoconch measurement PAT17 was defined in TURSCH & GERMAIN (1987).

Some operational quantitative characteristics are given in Table 1. As usual in species belonging to the genus *Oliva* (and contrary to widespread assumption), the most variable character is the relative height of the spire (H-L)/H.

Morphometric separation from *O. oliva*. This was effected by comparing 12 specimens of *O. ouini* (11 with intact protoconch) from the type locality to 100 specimens of *O. oliva* (L., 1758). These 100 specimens include 10 specimens of each of 10 different local populations, covering much of the inter-population variability of the species. At least half of each local sample consisted of shells less then 25 mm in length, to avoid the risk of size-related, artificial separations. The local phena, defined in TURSCH, MISSA & BOUILLON (1992), are: phenon *THA* (W. Thailand), phenon *AO* (W. Australia), phenon *BA* (Indonesia, Bali), phenon *SR* (Sri Lanka), phenon *HB* (Papua New Guinea, Hansa Bay), phenon *WJB* (Indonesia, West Java), phenon *WJA* (Indonesia, West Java), phenon *SJ* (Indonesia, South Java), phenon MB (Papua New Guinea, Milne Bay) and phenon *PA* (Philippines).

O. ouini can be completely separated from the morphological continuum of *O. oliva* (L., 1758). Only two examples will be given here: the scatter diagram of L/LW *vs.* D/H (see Fig. 1) and the scatter diagram of L/PNW *vs.*PAT17/RES5 (see Fig. 2).

The wide dispersion observed for the larger values of L/PNW in Fig. 2 corresponds to the non-isometric growth pattern of *O. oliva*, causing a marked increase of the relative length of the lip in large specimens (see TURSCH 1997).

	mean	min.	max.	S.D.	C.V.
Protoconch (*n* = 11) NW	3.59	3.40	3.90	0.180	5.0 %
RES5	1.16	1.13	1.21	0.027	2.3 %
PAT17	0.63	0.58	0.67	0.030	4.7 %
PAT17/RES5	0.54	0.50	0.57	0.023	4.3 %
Teleoconch (*n* = 12) D/H	0.40	0.38	0.43	0.015	3.9 %
D/L	0.54	0.53	0.57	0.012	2.2 %
L/H	0.74	0.70	0.78	0.024	3.3 %
L/LW	0.85	0.82	0.87	0.015	1.7 %
(H-L)/H	0.26	0.22	0.29	0.023	8.8 %
log(H)/PNW	0.78	0.75	0.82	0.023	3.0 %

Table 1. Some morphometric characteristics of *O. ouini* sp. nov. All specimens from type locality. S.D.: standard deviation; C.V. : coefficient of variation (100*SD/mean).

Diagnosis. A few easy identification tips are sketched in Pl. 2, Figs. 1,2.

Discussion. At first glance, *O. ouini* is similar in shape to some populations of *O. oliva*. The most obvious difference is the presence in *O. ouini* of 8-9 very strong, oblique columellar plications (see Pl. 1, Figs. 1-6), which are never observed in *O. oliva* (L., 1758) (see Pl. 1, Figs. 10-12) or in the closely related *O. tigridella* Duclos, 1835 (see Pl. 1, Fig. 9). The protoconchs of the two species are very similar (see Pl. 2, Figs. 3, 6) but the ratio PAT17/RES5 is mostly smaller in *O. ouini* (see Fig. 2). For the same size of shell lip, *O. ouini* has generally more postnuclear whorls than *O. oliva* (smaller L/PNW). The external contour of the lip is slightly more angulate.

O. ouini is immediately distinguished by its elongated, biconic body whorl from juveniles of the syntopic species *O. caerulea* (Röding, 1798) (see Pl. 1, Fig. 7) which has a completely different protoconch (see Pl. 2, Fig. 4) and from *O. concinna* Marrat, 1870 which has a somewhat similar protoconch (see Pl. 2, Fig. 5) but differs by many morphometric discriminants (measurements taken on juveniles with H < 25mm, *n*=9), amongst others L/LW (mean 0.93, max. 0.94; min. 0.92; S.D. 0.006; C.V. 0.63 %; compare with Table 1).

ANATOMY.

Four specimens were examined (Table 1). The radulae of two specimens were studied by SEM.

External anatomy. The body of a specimen with H: 11.6 mm consists of 2.5 postnuclear whorls, the mantle cavity spanning *ca.* 2/3 whorl (Pl. 6, Figs. A-B; Pl. 7, Figs. A-C). The live animal of *O. ouini* is yellow-beige, with very contrasting dark brown maculations on all the foot (see Pl. 2, Figs. 7-9). In alcohol-preserved specimens, the body is pale yellowish, siphon, head tentacles and propodium partially speckled with brownish spots. The foot is thin, folding longitudinally during fixation; posteriorly it forms a pouch (Pl. 6, Figs. A, B; Pl. 7, Fig. B, C - fp). The length of the columellar muscle is about one whorl.

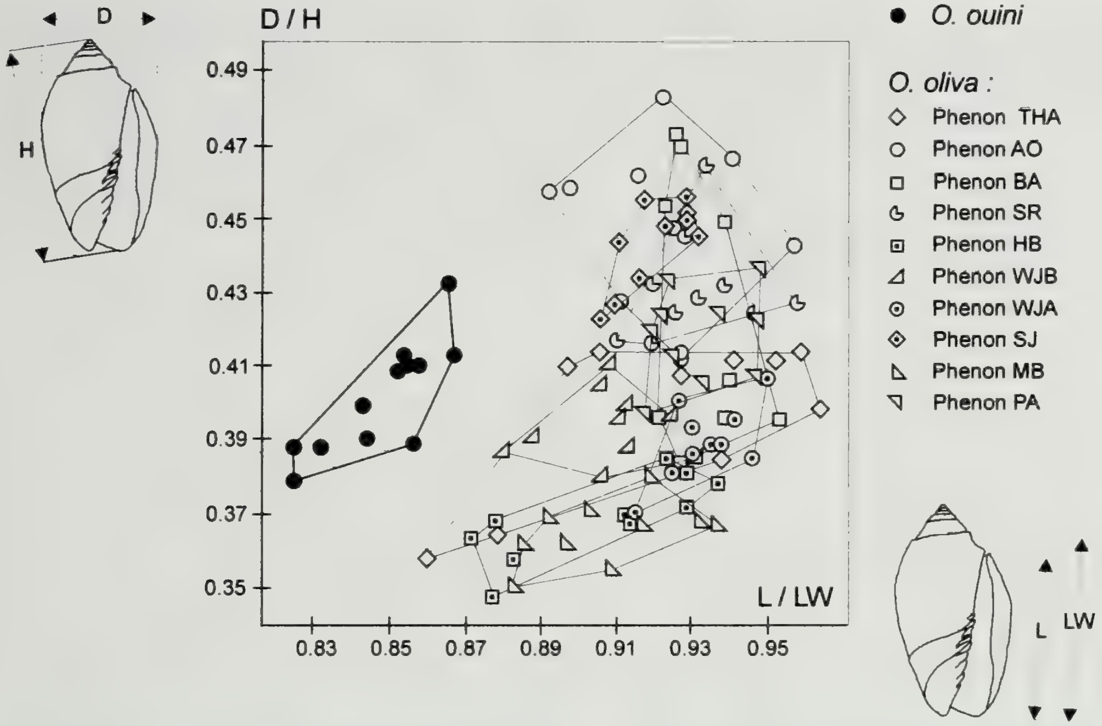

Fig. 1. Morphometric separation of *O. ouini* sp. nov. from *O. oliva* (L., 1758). Scatter diagram of L/LW *vs.* D/H. Minimum convex polygons. See text.

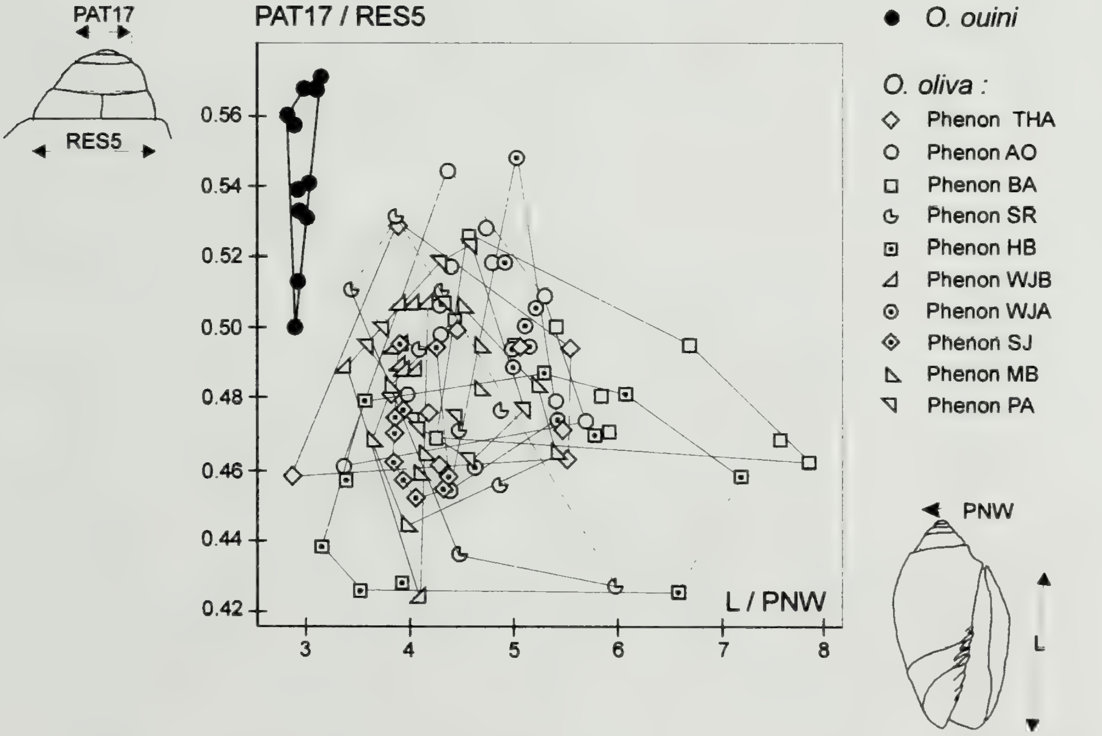

Fig. 2. Morphometric separation of *O. ouini* sp. nov. from *O. oliva* (L., 1758). Scatter diagram of L/PNW *vs.*PAT17/RES5. Minimum convex polygons. See text.

Mantle cavity (Pl. 6, Fig. D; Pl. 7, Fig. E). Mantle edge even. Mantle rather thick, although the osphradium and the ctenidium are seen through it. Siphon long with smooth edges, extending substantially (32% to 40% of L) beyond the mantle edge.

Osphradium yellowish, bipectinate, 55% to110% (mean: 88%; σ: 0.23) of the width and 74% to 88% (mean: 81%; σ: 0.07) of the length of the large, deeply hanging ctenidium. Osphradium asymmetrical: there are more lamellae on the right side than on the left (Table 2) (in average 54 *vs.* 47). The ctenidium occupies nearly 4/5 of mantle length. Hypobranchial gland moderately glandular, forming very low transverse folds. Anterior mantle tentacle flat, may be nearly as long as the siphon. Posterior mantle tentacle not pigmented, moderately long, about half of the lip length (L). Mantle lobe small, concave.

Rectal gland absent.

shell length, mm	aperture length, mm	number of radular rows	number of forming radular rows	radular width	rachidian width	number of ctenidium lamellae	ctenidium width, mm	ctenidium length, mm	number of osphradium lamellae, left part	number of osphradium lamellae, right part	osphradium width, mm	osphradium length, mm	sex, maturation
11.3	8.5	80	12	0.12	0.04	85	1.0	4.3	45	53	0.9	3.2	♀, mature
11.6	8.6	?	?	0.11	0.04	70	1.0	3.4	41	50	1.0	2.9	♂, mature
11.8	9.0	90	25	0.12	0.03	95	1.8	4.0	50	65	1.0	3.5	♂, mature
13.9	10.1	91	25	0.13	0.05	85	1.2	4.3	46	48	1.3	3.3	♀, mature

Table 2. *Oliva ouini* sp. nov. Summary of some anatomical characters examined. All from type locality.

shell length, mm	aperture length, mm	number of radular rows	number of forming radular rows	radular width	rachidian width	number of ctenidium lamellae	ctenidium width, mm	ctenidium length, mm	number of osphradium lamellae, left part	number of osphradium lamellae, right part	osphradium width, mm	osphradium length, mm	sex, maturation
11.6	8.5	?	?	?	?	87	1.25	4.0	47	62	0.8	3.4	♀, immature
12.3	8.8	132	42	0.16	0.06	90	1.5	4.2	54	65	0.9	3.6	♀, immature
12.8	?	138	25	0.16	0.03	95	?	?	?	?	?	?	?
13.1	9.1	?	?	?	?	?	1.2	3.0	?	?	1.0	2.3	♂, immature
14.1	10.3	146	35	0.13	0.04	95	1.3	3.8	46	60	0.8	3.0	♂, immature
15.8	11.4	174	41	0.13	0.04	90	1.5	4.3	55	60	0.8	3.3	♂, mature
18.5	14.6	158	?	0.15	0.05	?	?	?	?	?	?	?	?
19.2	14.0	?	?	?	?	110	2.2	4.2	62	80	1.0	3.4	♀, mature
19.9	14.4	?	?	?	?	?	2.1	4.2	?	?	1.1	2.8	♀, mature
20.2	14.8	?	?	?	?	105	1.9	5.1	55	60	1.0	3.1	♀, mature
21.8	18.5	175	?	0.16	0.06	?	?	?	?	?	?	?	?
22.0	17.3	?	?	?	?	127	2.7	5.5	55	74	1.2	3.5	♀, mature
22.9	19.2	156	?	0.18	0.07	?	?	?	?	?	?	?	?
23.0	19.7	184	?	0.17	0.06	?	?	?	?	?	?	?	?
25.8	18.6	?	?	?	?	145	3.2	6.1	73	70	1.3	4.5	♂, mature
27.0	19.5	168	41	0.27	0.09	?	?	?	?	?	?	?	♂, mature
33.4	?	?	?	0.28	0.09	185	4.1	10.3	88	100	1.3	7.5	♀ mature

Table 3. *Oliva oliva* (L., 1758). Summary of some anatomical characters examined. Papua New Guinea, Hansa Bay: last two specimens from Boro Beach, all others from Sisimangum Beach.

Digestive system. One specimen (female, H: 13.9 mm) was preserved with its proboscis everted (Pl. 7, Fig. H). Proboscis not long [17% of H when contracted (Pl. 6, Fig. F) to 25% of H when everted], narrow (length/diameter ~ 4.5-7), and lies within the thin-walled proboscis sheath.

The foregut of *O. ouini* is generally very similar to that of *O. oliva*.

The radula consists of 80 (specimen H: 11.3 mm) to 91 (specimen H: 13.9 mm) rows of teeth, of which 12-25 rows are not yet completely chitinized. Radula width varies from 0.91% to1.06% of H (mean: 0.97%; σ: 0.07; n=4). The lateral teeth are very similar in shape to that of *O.oliva*. Rachidian teeth: the lateral sides of the basal part fuse with the subradular membrane and are inconspicuous. In dorsal view, the anterior edges of the basal parts are nearly straight or very slightly concave in the middle. The rachidian teeth have 3 cusps, the central one being the smallest.

Stomach small, with long caecum and single duct of the digestive gland. The shape of stomach differs greatly amongst specimens. We were unable to examine the stomach anatomy.

Reproductive system. The gonad, together with the digestive gland, occupies the upper whorls of the visceral mass, starting at the level of the stomach (Pl. 6, Figs. C, H; Pl. 7, Fig. F - gon). The gonad is not overlaid by the digestive gland. The penis is large, bilobed, with a somewhat flattened basal lobe and a rounded upper lobe which terminates in small curved seminal papilla (Pl. 6, Figs. E, G). The smallest studied specimen (H: 11.6 mm) had a fully formed penis, indicating that the specimen was mature. The smallest studied female (H: 11.3 mm) had large, fully developed pallial gonoduct (Pl. 7, Fig. E - pgon). It can thus be concluded that *O. ouini* reaches sexual maturity at a shell length of less than 11.3 mm.

Comparison with *O. oliva*.
In spite of the general similarity of their anatomy, the two species differ by at least four independent anatomical characters.

1. The radula of *O. ouini* has a significantly smaller number of teeth rows (80-91 *vs.* 132-184 for *O. oliva*, see Tables 2 and 3).

2. The rachidian radular teeth differ in shape: in *O. oliva* the anterior edge is markedly convex (see Pl. 8), in *O. ouini* it is nearly straight and even concave in the middle (see Pl. 9).

3. In *O. oliva* the gonad starts at the level of the nephridium (see Pl. 5, Fig. B); in *O. ouini* it starts at the level of the stomach (Pl. 6, Figs. C,H; Pl. 7, Fig. F).

4. The shape of the penis of *O. oliva* (see Pl. 5, Figs. G, H) is very different from that of *O. ouini* (see Pl. 6, Figs. E, G).

5. The strong maculations seen on the live animal of *O. ouini* are not observed on the body of *O. oliva* which comes in different colours, generally matching the ground colour of the shell (see Pl. 2, Figs. 10-13).

It was also shown that *O. ouini* reaches maturity at a size at least 3.5 mm smaller than *O. oliva*. Other differences (such as the size of the anterior and posterior mantle tentacles) are small and may depend on the conditions of preservation.

OTHER DATA.

Distribution. For years, known only from the type locality, where it is confined to a very small area. The distribution range is in fact much wider. Seven nearly identical specimens originating from Vanuatu [given locality: "Ambre Isl." (error for Ambrym ?),1-3 m] have now been identified in the collection of Mr. J.P. LEFORT (Tahiti) by Dr. Dietmar GREIFENEDER who also has one specimen from Vanuatu, "plage" (2.5 m, black sand).

Habitat. In Papua New Guinea *O. ouini* has been found only in rather calm water, fine grey coral sand, 6-7 m, around one of the ship wrecks in Hansa Bay. It is there syntopic with other *Oliva* species, amongst others *O. caerulea* (Röding, 1798), *O. concinna* Marrat, 1870, *O. reticulata* (Röding, 1798), *O. sericea* (Röding, 1798). In contrast, *O. oliva* is confined to open sand beaches, exposed to occasional strong surf.

In Vanuatu, *O. ouini* is reported from 1 to 3 m depth.

Etymology. This species is named for our friend Jean-Marc OUIN, former manager of Laing Island Biological Station and master in the art of finding elusive *Oliva* species.

Acknowledgements.
We are grateful to the Belgian Fonds National de la Recherche Scientifique (F.N.R.S.) and to BIOTEC, S.A. for supporting our research. We thank Dr. Dietmar GREIFENEDER for much advise.

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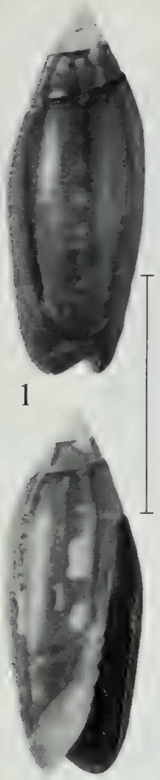
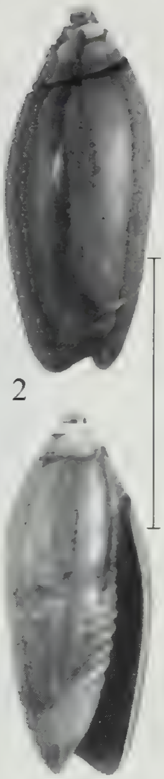
Plate 1. Scale bars: 10 mm.

- **1-6.** ***O. ouini*** sp. nov. All from type locality.
  - **1.** Holotype (H: 15.62 mm; D: 5.91 mm): BM(NH).
  - **2.** Paratype 1 (H: 13.50 mm; D: 5.51 mm): IRNSB.
  - **3.** Paratype 2 (H: 13.59 mm; D: 5.57 mm): ZMM n°.Lc 23326.
  - **4.** Paratype 3 (H: 13.66 mm; D: 5.64 mm): USNM.
  - **5.** Paratype 4 (H: 12.91 mm; D: 5.04 mm): MNHN.
  - **6.** Paratype 5 (H: 12.05 mm; D: 4.97 mm): AMS.
- **7.** ***O. caerulea*** (Röding, 1798). Juvenile shell (H: 14.77 mm; D: 6.46 mm), found together with *O. ouini*, in type locality.
- **8.** ***O. concinna*** Marrat, 1870. Juvenile shell (H: 14.82 mm; D: 5.96 mm), found together with *O. ouini*, in type locality.
- **9.** ***O. tigridella*** Duclos, 1840. Juvenile shell (H: 16.84mm; D: 6.77 mm), Philippines, Cebu.
- **10-12.** ***O. oliva*** (L., 1758).
  - **10.** Juvenile shell (H: 15.81 mm; D: 5.77 mm), Papua New Guinea, Hansa Bay, Sisimangum Beach, low tide.
  - **11.** Juvenile shell (H: 19.92 mm; D: 8.33 mm), Vietnam, Nha Trang, Hon Tre Is., low tide.
  - **12.** Juvenile shell (H: 15.66 mm; D: 6.43 mm), Sri Lanka, Welligama, low tide.



1

holotype



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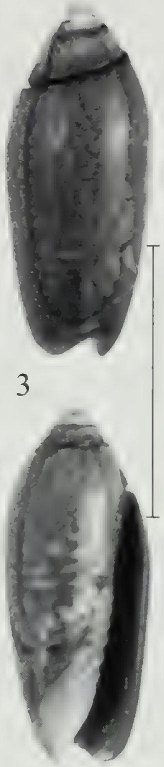
paratype 1



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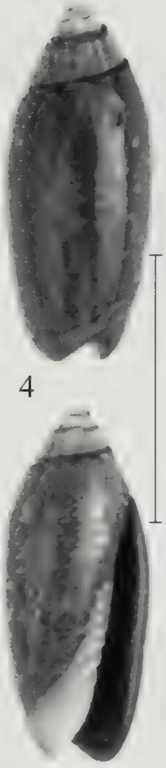
paratype 2



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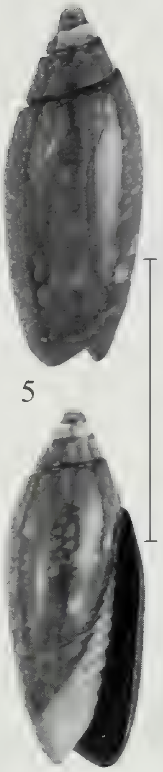
paratype 3



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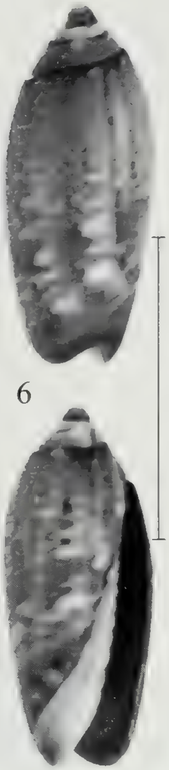
paratype 4



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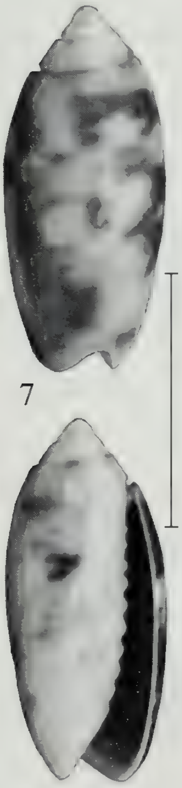
paratype 5

O. ouini sp. nov.



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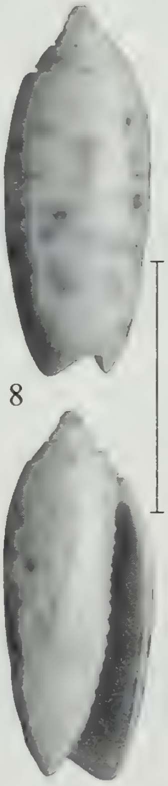
O. caerulea



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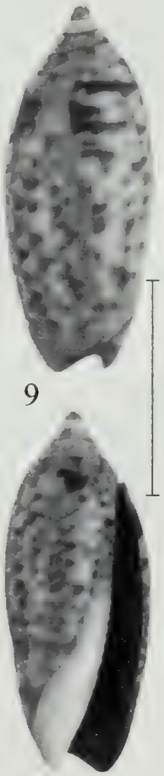
O. concinna



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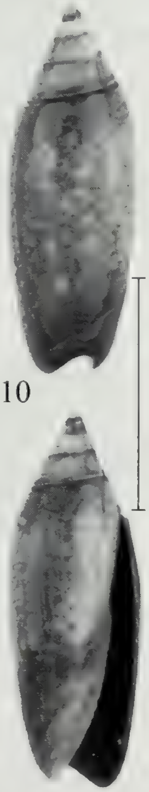
O. tigridella



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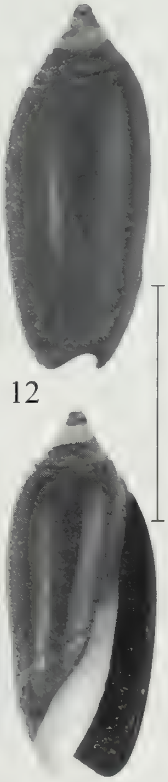


12

O. oliva

Plate 2.

1-3. ***O. ouini*** sp. nov. All from type locality.
  1.-2. Tips for quick shell recognition.
  3. Protoconch.

4. ***O. caerulea*** (Röding, 1798). Protoconch. Juvenile shell (H: 14.77 mm; D: 6.46 mm), found together with *O. ouini*, in type locality.

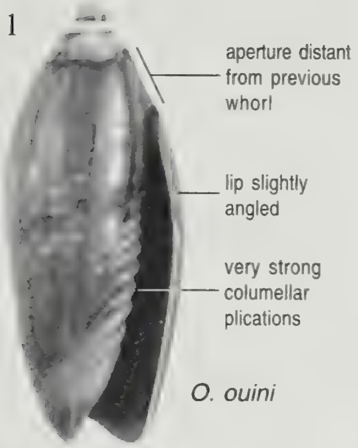
5. ***O. concinna*** Marrat, 1870. Protoconch. Juvenile shell (H: 14.82 mm; D: 5.96 mm), found together with *O. ouini*, in type locality.

6. ***O. oliva*** (L., 1758). Protoconch. Juvenile shell (H: 15.81 mm; D: 5.77 mm), Papua New Guinea, Hansa Bay, Sisimangum Beach, low tide. Juvenile shell (H: 15.81 mm; D: 5.77 mm), Papua New Guinea, Hansa Bay, Sisimangum Beach, low tide.

7-9. ***O. ouini*** sp. nov. Live animals. All from type locality.

10-13. ***O. oliva*** (L., 1758). Live animals, different colour forms, all from Papua New Guinea, Hansa Bay, Sisimangum Beach, low tide.

1



O. ouini

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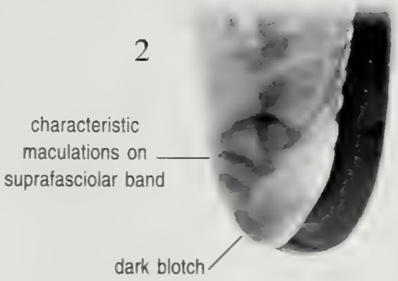

O. ouini

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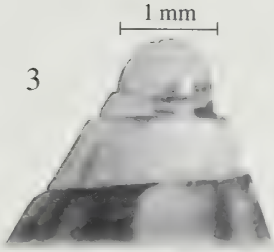

O. ouini

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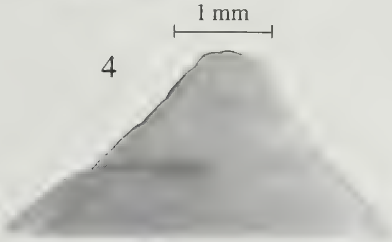

O. caerulea

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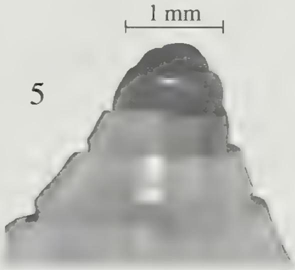

O. concinna

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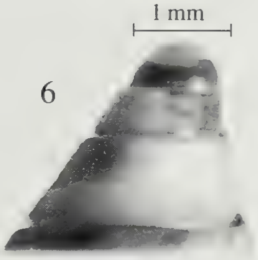

O. oliva

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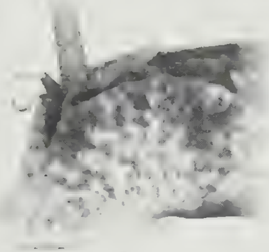

O. ouini

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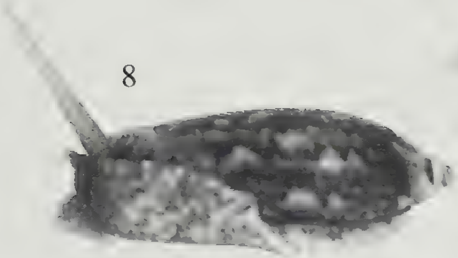

O. ouini

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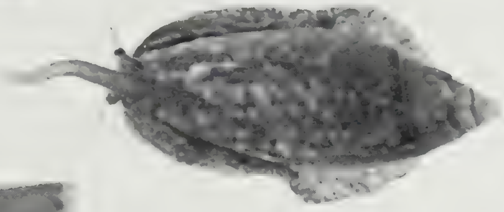

O. ouini

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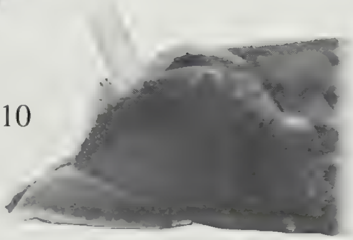

O. oliva

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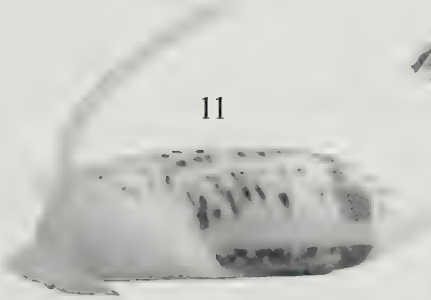

O. oliva

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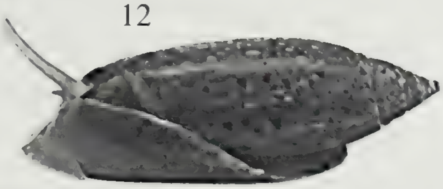

O. oliva

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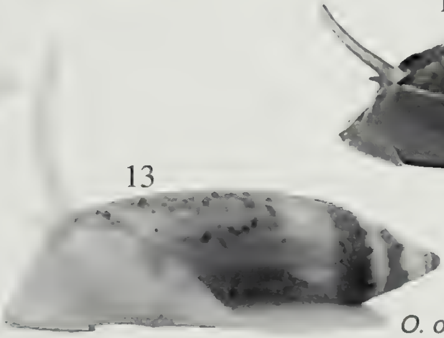

O. oliva

Plate 3. Anatomy of *O. oliva* (L., 1758).

Specimen(♂ H: 15.8 mm) from Papua New Guinea, Hansa Bay, Sisimangum Beach.

Scale bars: A, B - 2 mm, C-F - 1 mm.

A, B - body removed from the shell.

C - view of visceral mass, showing the shape of stomach.

D - cut-out mantle.

E - anterior part of digestive system from the right side with the proboscis everted, extended.

F - native position of the gland of Leiblein and salivary glands, from the left anterior side.

amt - anterior mantle tentacle
ao - anterior aorta
asg - accessory salivary gland
cm - columellar muscle
cme - cut mantle edge
ct - ctenidium
dasg - duct of accessory salivary gland
ddg - duct of digestive gland
dg - digestive gland
dgL - duct of gland of Leiblein
fp - pouch of foot
gL - gland of Leiblein
gon - gonad
hg - hypobranchial gland
ml - mantle lobe
nr - nervous ring
os - osphradium
par - parapodium
pen - penis
pmt - posterior mantle tentacle
poe - posterior oesophagus
pr - proboscis
prp - propodium
re - rectum
s - siphon
sd - salivary duct
sg - salivary gland
st - stomach
vL - valve of Leiblein

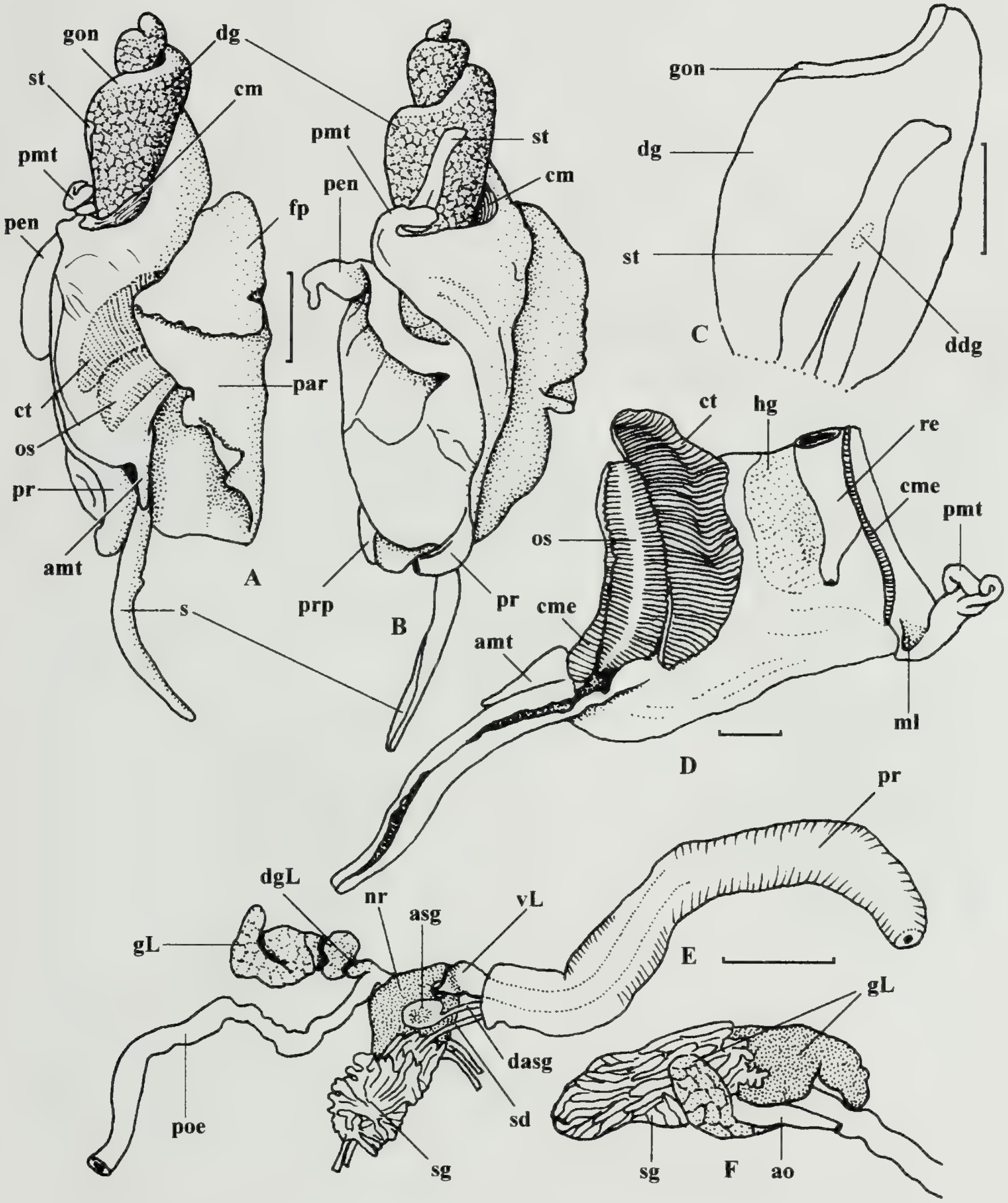

Plate 3. *Oliva oliva* (L., 1758)

Plate 4. Anatomy of *O. oliva* (L., 1758).

A-D -Specimen (♀ H: 33.4 mm) from Papua New Guinea, Hansa Bay, Boro Beach.
Scale bars: A, B, D - 5 mm, C - 2 mm, F - 1 mm, E - 0.5 mm.

A, B - body removed from the shell.

C - stomach, opened dorsally.

D - cut-out mantle.

E - Shape of ctenidium lamellae. Specimen (H: 13.1 mm) from Papua New Guinea, Hansa Bay, Sisimangum Beach.

F - Shape of ctenidium lamellae. Specimen (H: 22.0 mm) from Papua New Guinea, Hansa Bay, Sisimangum Beach.

amt - anterior mantle tentacle
c - caecum of the stomach
cm - columellar muscle
cme - cut mantle edge
ct - ctenidium
ddg - duct of digestive gland
dg - digestive gland
gon - gonad
ht - head tentacles
ig - intestinal groove
ml - mantle lobe
oe - oesophagus
os - osphradium
pgon - pallial gonoduct
pmt - posterior mantle tentacle
prp - propodium
psa - posterior sorting area
re - rectum
s - siphon
st - stomach
t - typhlosoles

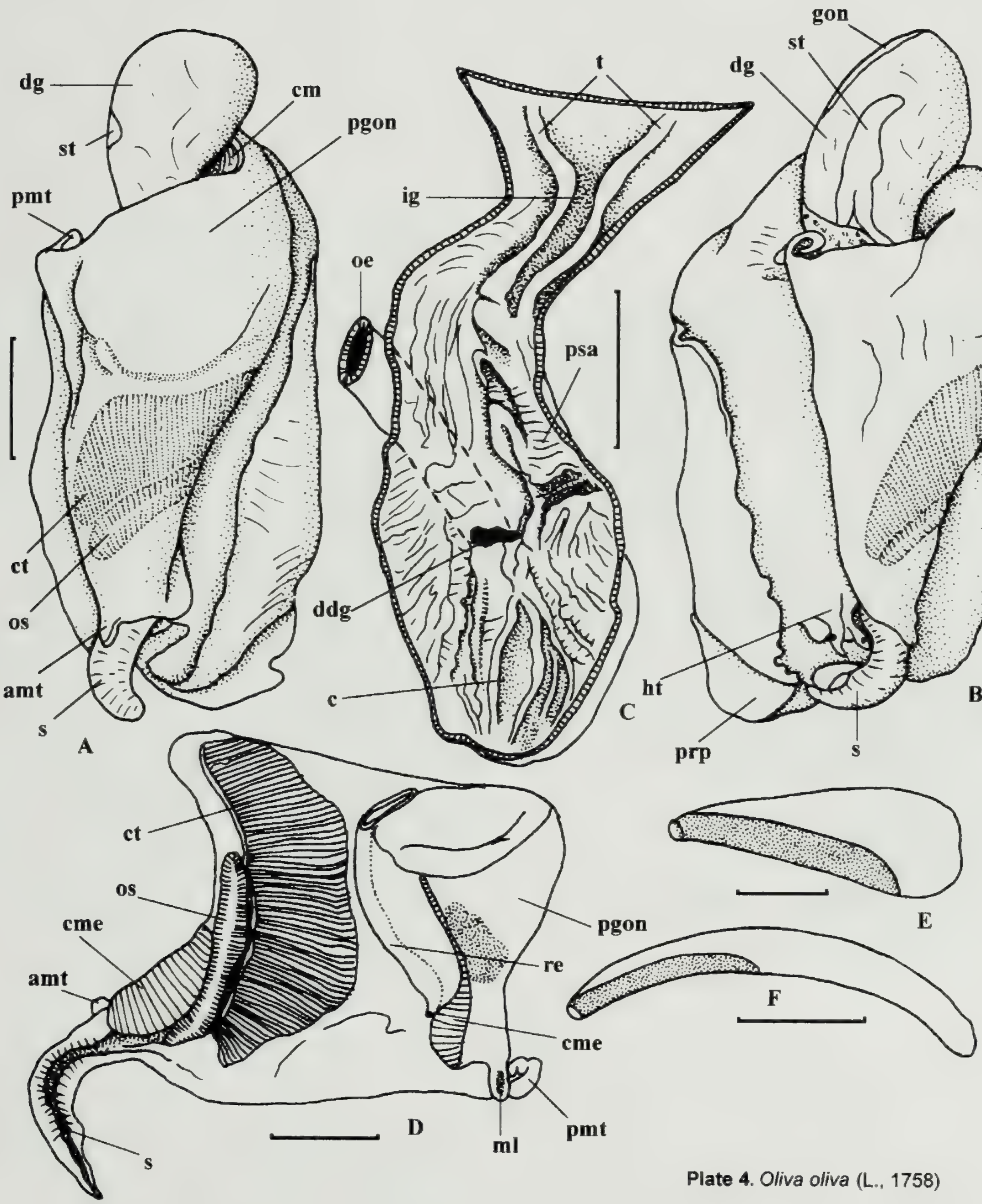

Plate 4. *Oliva oliva* (L., 1758)

Plate 5. Anatomy of *O. oliva* (L., 1758). Scale bars: A,B - 2 mm, C-F - 1 mm.

Specimens from Papua New Guinea, Hansa Bay, Sisimangum Beach.
A, H - (♂ H: 14.1 mm) (drawn to the same scale).
B, E - (♀ H: 11.43 mm) (drawn to the same scale).
C,F,G - (♂ H: 25.8 mm).
D - (♂ H: 19.2 mm).
Scale bars: 1 mm.

A-D - views of visceral mass, showing variability of the shape of stomach.

E - anterior part of digestive system from the right side, extended.

F - stomach, opened dorsally.

G, H - ontogenetic changes of the penis shape and size.

asg - accessory salivary gland
c - caecum of the stomach
ddg - duct of digestive gland
dgL - duct of gland of Leiblein
gL - gland of Leiblein
gon - gonad
ig - intestinal groove
nr - nervous ring
od - odontophore
ooe - opening of oesophagus into stomach
poe - posterior oesophagus
pr - proboscis
prr - proboscis retractors
psa - posterior sorting area
rhd - rhynchodaeum (proboscis sheath)
rs - radular sac
sg - salivary gland
t - typhlosoles
vL - valve of Leiblein

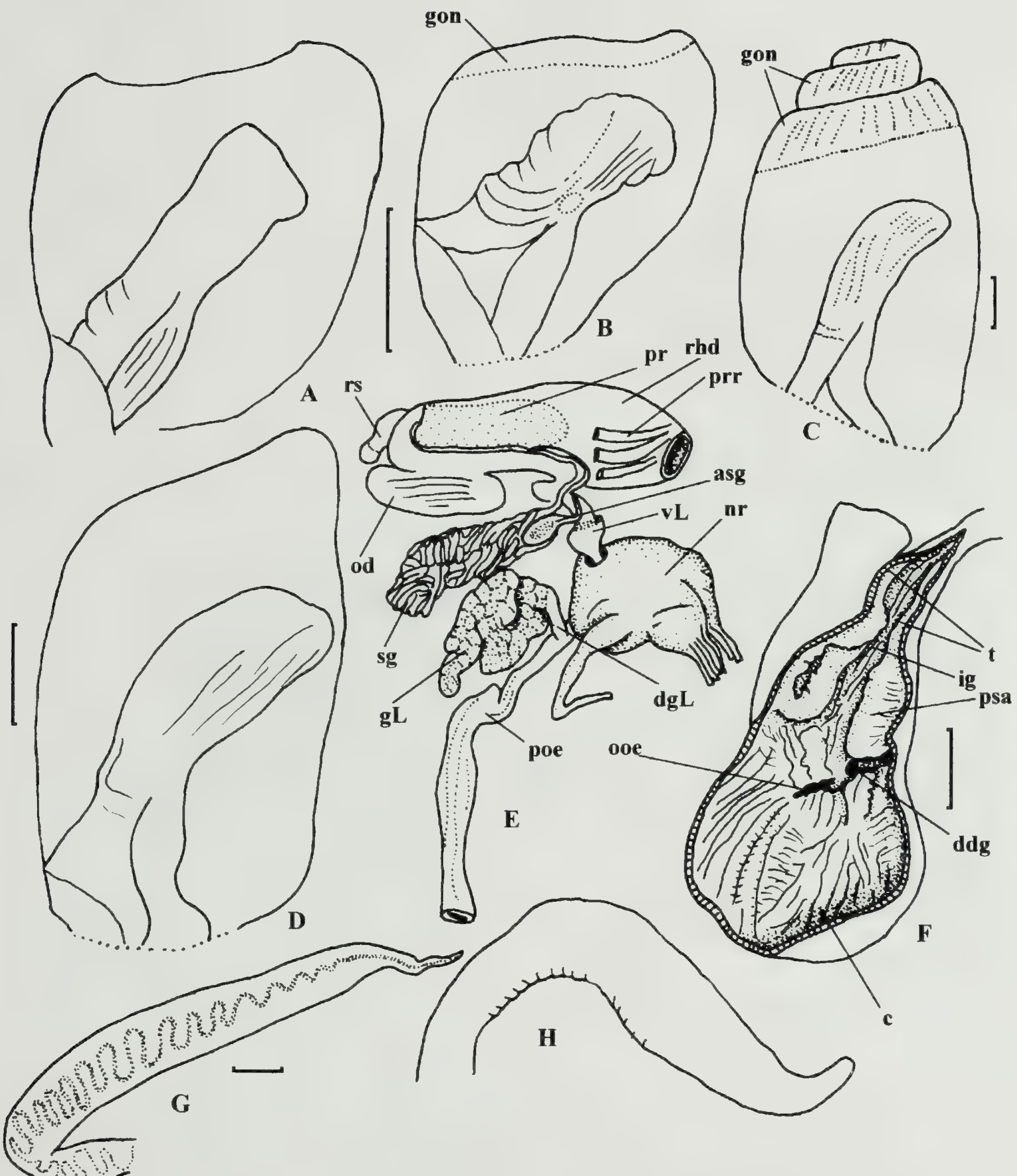

Plate 5. *Oliva oliva* (L., 1758)

Plate 6. Anatomy of males of *Oliva ouini* sp. nov.

A-F: (♂ H: 11.6 mm); G-H: (♂ H: 11.8 mm).

Scale bars: A,B - 2 mm; others - 1 mm. C, F, H drawn to the same scale.

A,B - body removed from the shell.

C,H - view of visceral mass, showing the shape of stomach.

D - cut-out mantle.

E, G - penis.

F - anterior part of digestive system from the right side, extended. Proboscis inside the rhynchodaeum is shown by dotted line.

amt - anterior mantle tentacle
asg - accessory salivary gland
cm - columellar muscle
cme - cut mantle edge
ct - ctenidium
dasg - duct of accessory salivary gland
dg - digestive gland
dgL - duct of gland of Leiblein
fp - pouch of foot
gL - gland of Leiblein
gon - gonad
hg - hypobranchial gland
ht - head tentacles
ml - mantle lobe
nr - nervous ring
oe - oesophagus
os - osphradium
par - parapodium
per - pericardium
pmt - posterior mantle tentacle
poe - posterior oesophagus
pr - proboscis
prp - propodium
prr - proboscis retractors
re - rectum
rhd - rhynchodaeum (proboscis sheath)
s - siphon
sg - salivary gland
st - stomach
vL - valve of Leiblein

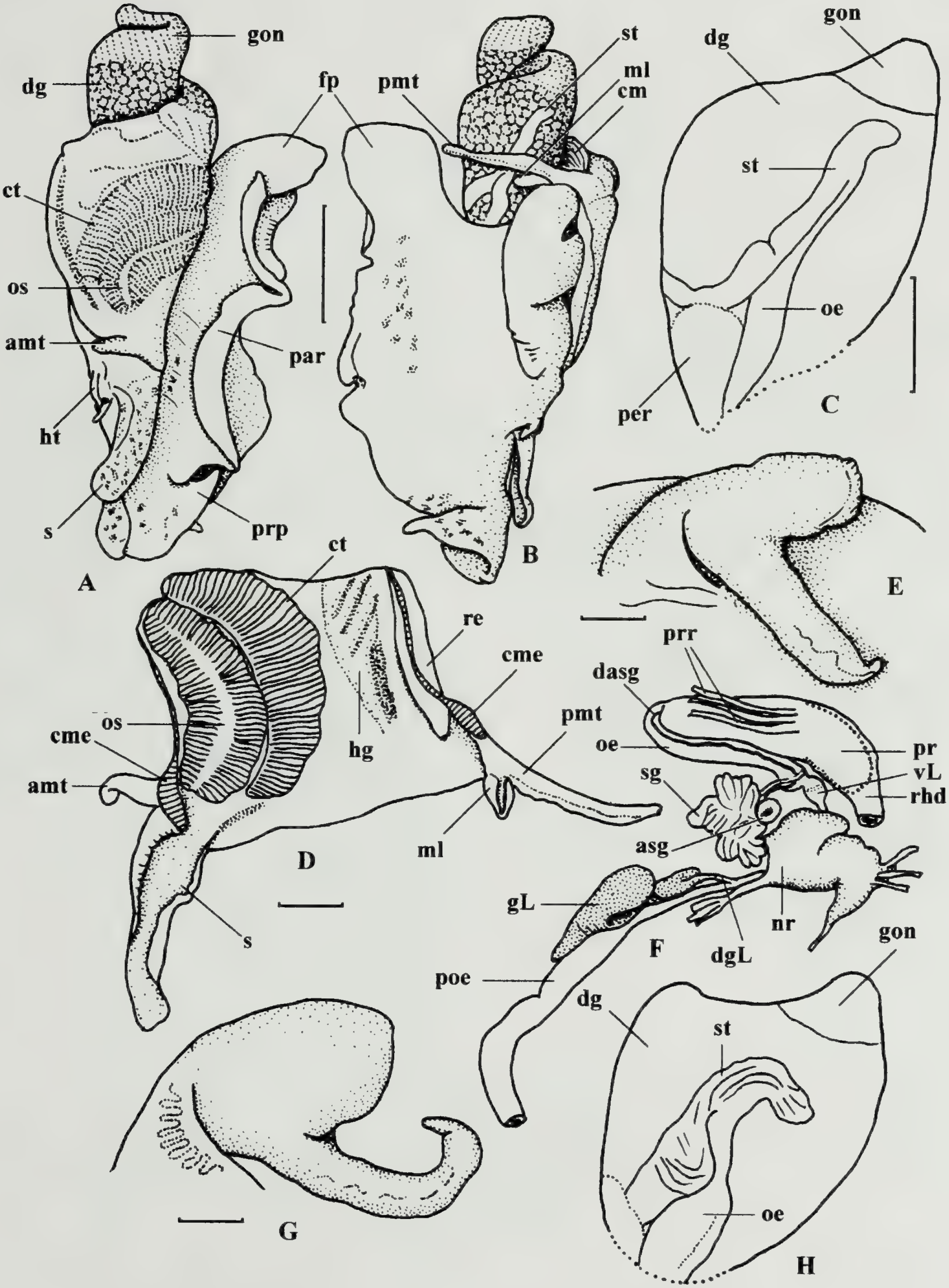

Plate 6. *Oliva ouini* sp. nov.

Plate 7. Anatomy of a female of *Oliva ouini* sp. nov., (H: 13.9 mm).
Scale bars: A, B, C, E - 2 mm; F, G, H - 1 mm.

A, B - body removed from the shell.
C - ventral view of the foot, showing the ventral pedal gland.
D - enlarged dorsal view of the head with proboscis protruded.
E - cut-out mantle.
F - view of visceral mass, showing the shape of stomach.
G - stomach from inner side.
H - anterior part of digestive system, from the right side, extended.

amt - anterior mantle tentacle
asg - accessory salivary gland
cme - cut mantle edge
ct - ctenidium
dasg - duct of accessory salivary gland
ddg - duct of digestive gland
dg - digestive gland
dgL - duct of gland of Leiblein
fp - pouch of foot
gL - gland of Leiblein
gon - gonad
hg - hypobranchial gland
ht - head tentacles
ml - mantle lobe
nr - nervous ring
oe - oesophagus
os - osphradium
par - parapodium
pgon - pallial gonoduct
pmt - posterior mantle tentacle
poe - posterior oesophagus
pr - proboscis
prp - propodium
re - rectum
s - siphon
sg - salivary gland
st - stomach
vL - valve of Leiblein
vpg - ventral pedal gland.

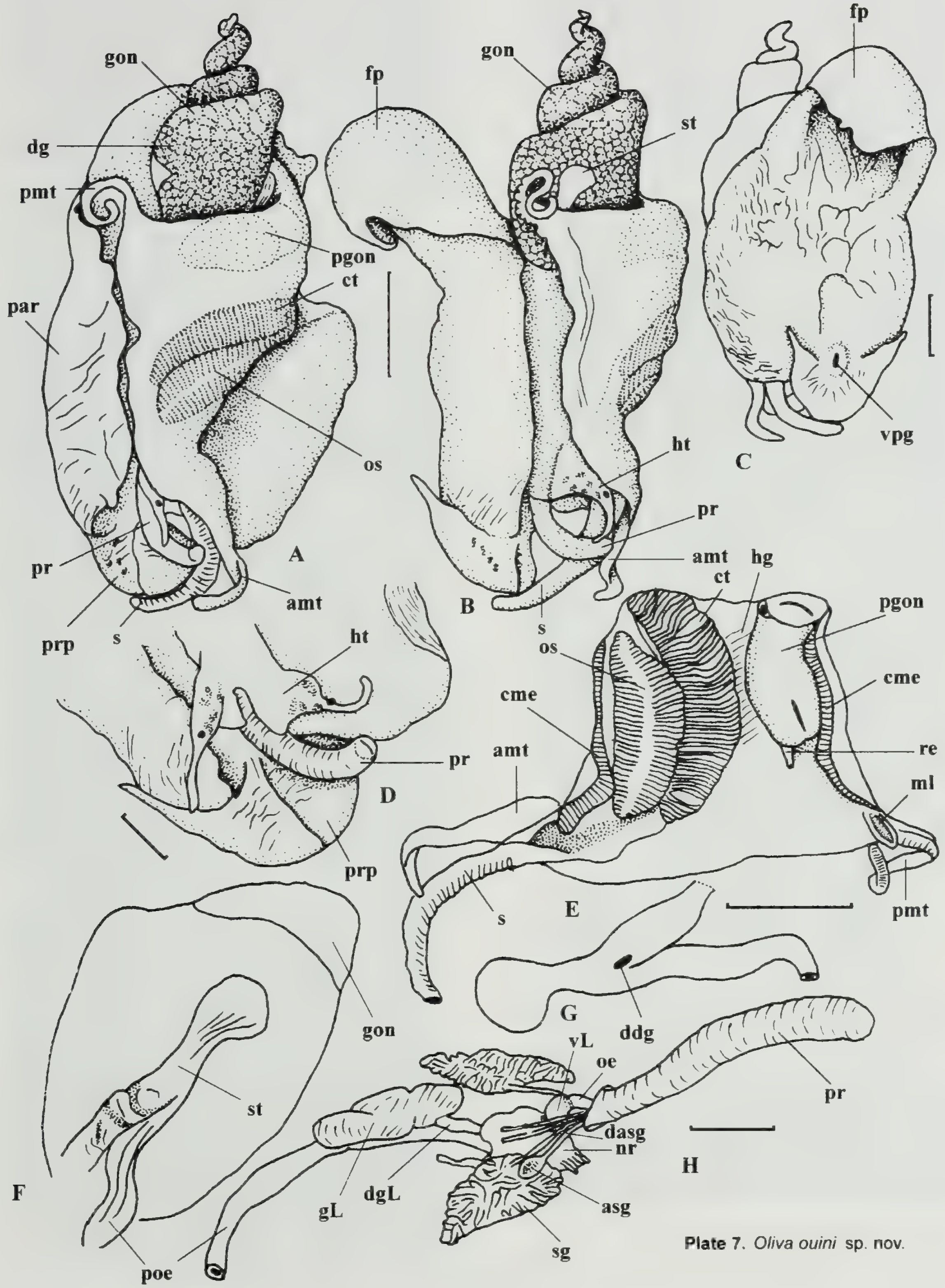

Plate 7. *Oliva ouini* sp. nov.

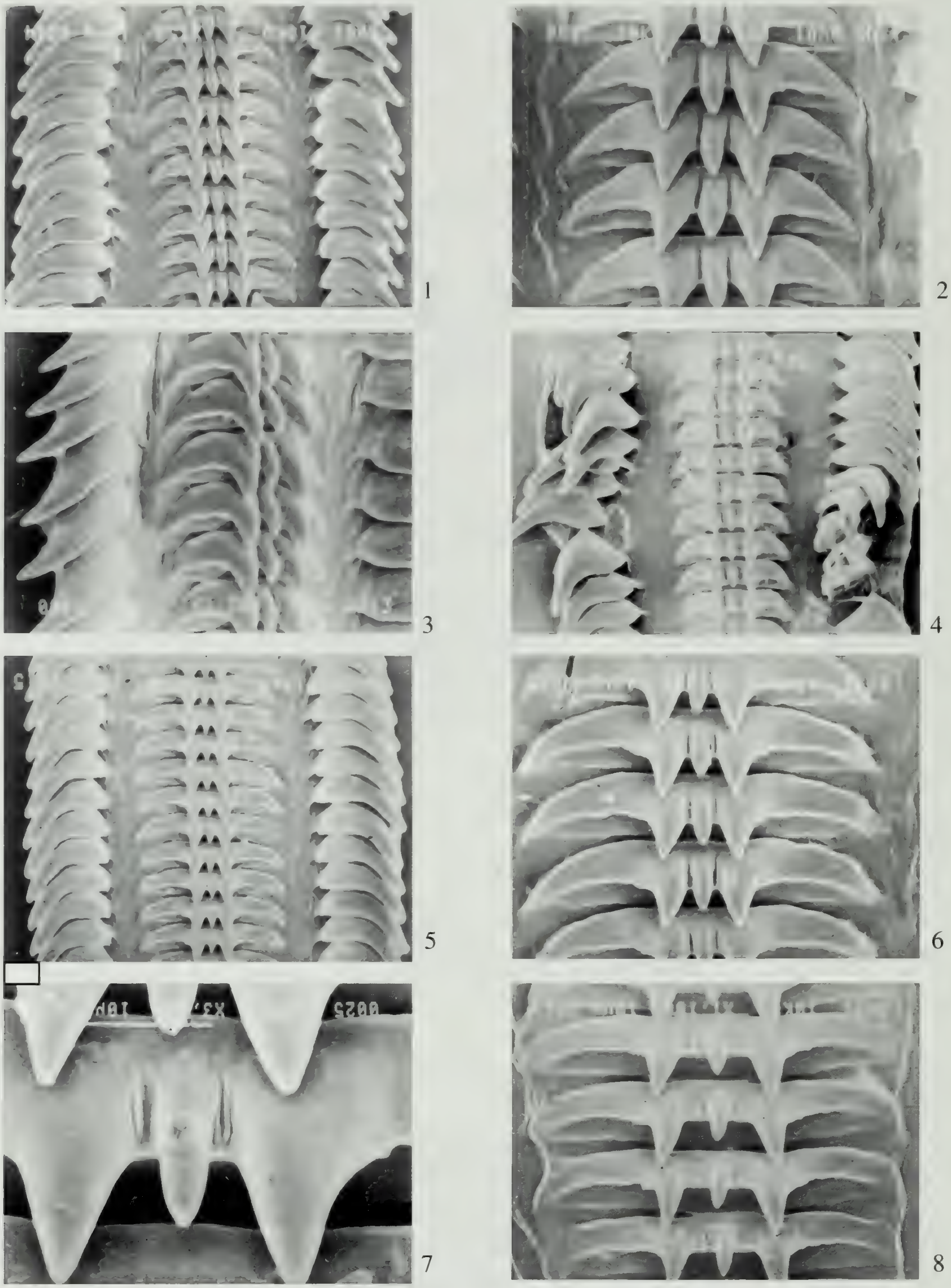

Plate 8. *Oliva oliva* (L., 1758).

1-3: female, Papua New Guinea, Hansa Bay, Sisimangum (H: 11.6 mm).

4: female, Papua New Guinea, Hansa Bay, Sisimangum (H: 20.2 mm).

5-7: male, Papua New Guinea, Hansa Bay, Boro Beach (H: 27.0mm).

8: female, Papua New Guinea, Hansa Bay, Boro Beach (H: 33.4 mm).

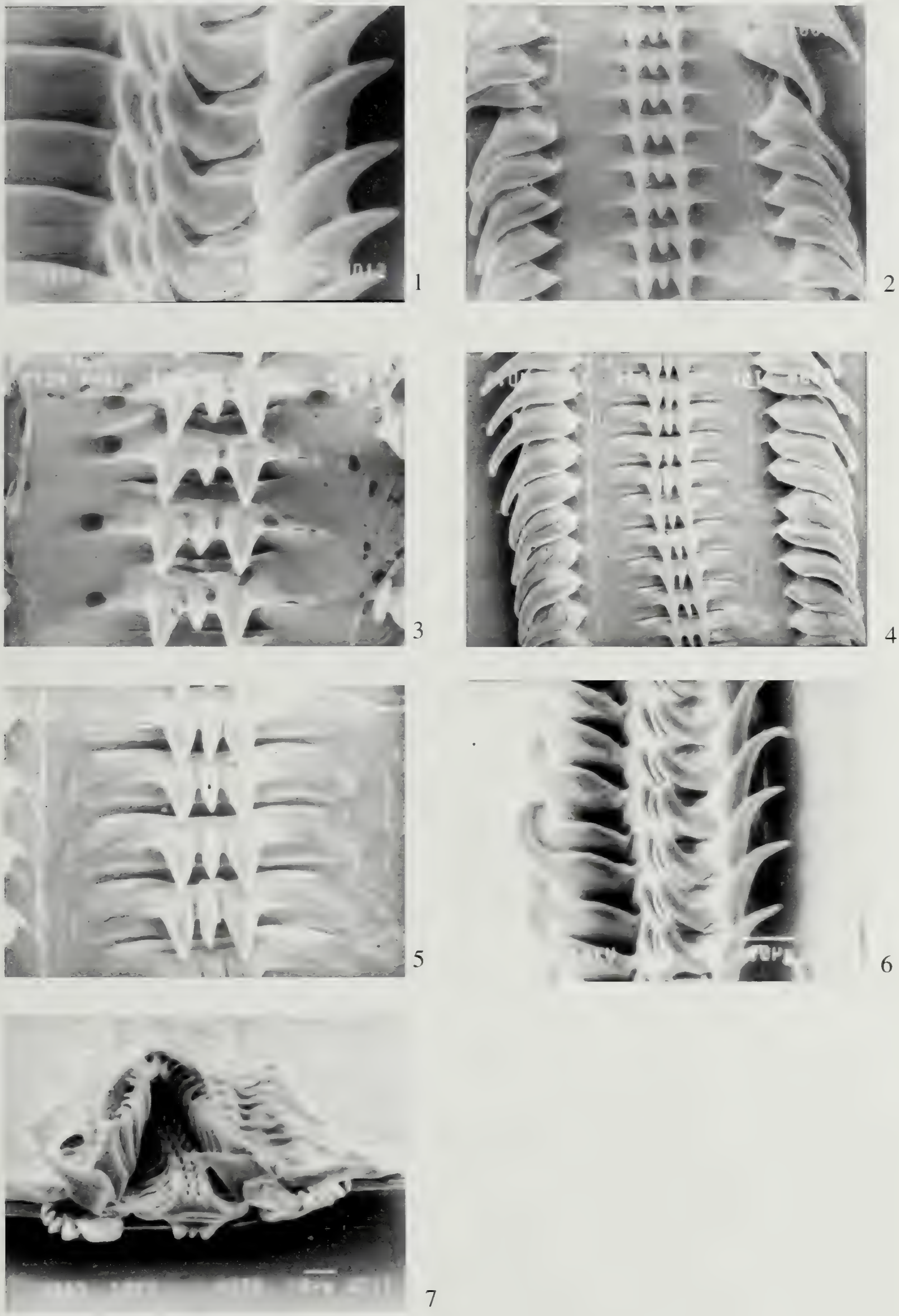

Plate 9. *Oliva ouini* sp. nov. All from type locality.

1-3: female (H: 11.3 mm).

4-7: male (H: 11.6 mm).

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Description of four new neogastropods of superfamilies Muricoidea and Conoidea from South Africa (Gastropoda: Prosobranchia: Neogastropoda)

R. N. KILBURN

Natal Museum, P/Bag 9070, Pietermaritzburg 3200, South Africa

KEYWORDS. Gastropoda, Columbellidae, Olividae, Drilliidae, Turridae, South Africa.

ABSTRACT. The following four Neogastropoda are described from the continental shelf or slope of eastern South Africa: *Anachis (Suturoglypta) blignautae* (family Columbellidae) from off southern Zululand; *Ancillista depontesi* (Olividae), *Splendrillia hayesi* (Drilliidae), and *Turris faleiroi* (Turridae) from the eastern Agulhas Bank. *Turris faleiroi* is the first temperate-water member of its genus known.

INTRODUCTION

The discovery of a notable proportion of the more striking southern African benthic molluscs is due to the activities of commercial fishing boats. Several such species, recently submitted to the Natal Museum by Mr Brian Hayes of Port Elizabeth, prove to be undescribed. Three of the species described here may be assumed from their known distribution to be temperate-water Agulhas Bank endemics, the fourth (an *Anachis*) may possibly prove to be a tropical East African element.

Abbreviations

BMNH: The Natural History Museum, London

NMSA: Natal Museum, South Africa

ZMHB: Zoological Museum, Humboldt University, Berlin.

TAXONOMY

Superfamily **MURICOIDEA**
Family **COLUMBELLIDAE**
Genus *Anachis* H. & A. Adams, 1853

The following species is referred to the subgenus *Suturoglypta* Radwin, 1968 [type species (o.d.) *Columbella pretri* Duclos, 1846], on account of its square-cut whorls. Nevertheless, this may prove to be a homoplasy, as the only three species previously referred to this subgenus all inhabit the western Atlantic region. These were discussed by Radwin (1978: 340), who elevated *Suturoglypta* to full genus status. In the absence of a modern analysis of the systematics of the Columbellidae, I prefer to follow a conservative approach.

Anachis (Suturoglypta) blignautae n. sp.
Figs 1-2

Type material.

Holotype NMSA V6140/T1548. Paratype 1, NMSA V6141/T1549; paratype 2 in B. Hayes collection. All taken from crayfish traps; paratypes both juvenile.

Type locality.

Off Richards Bay (c. 28°48'S, 32°05'E), 600 m.

Distribution.

Continental slope of southern Zululand, known only from the type locality.

Diagnosis.

Shell fusiform (aperture/total length 0.50), with a produced, somewhat dorsally bent anterior end, suture shallow; axial ribs strong, 12-13 per whorl, projecting most at periphery of last whorl, evanescing on base, crossed above and below suture by a spiral thread, which make spire whorls appear almost flat-sided; base of last whorl with 14 spiral threads; aperture with smooth margins, columella callus with slightly raised outer edge; siphonal canal not indented. Protoconch papillose, smooth, breadth 0.63-0.70 mm. Pale pinkish-orange, ribs and subsutural region white, protoconch 1 with a brown spot. Maximum length 11.2 mm.

Description.

Shell fusiform, of 6 teleoconch whorls, breadth/length 0.39, with a high, acute, orthoconoid spire (slightly cyrtoconoid towards apex) and a tapering, elongated anterior end; spire whorls rather flat-sided (almost quadrate), suture shallow. Aperture long (aperture/total length 0.50), narrow, greatest width at about posterior third, siphonal canal long and bent dorsally and to left, base obliquely truncate, termination not indented; inner and outer lips smooth, inner lip with a moderately thick callus, whose outer edge is slightly raised on columella; outer lip sinuous in side-view, evenly convex medially, shallowly concave below suture.

Sculptured by moderately strong axial ribs, crossed above and below suture by a spiral lira, base of last whorl spirally lirate. Axial ribs opisthocline, rather straight, in cross-section rounded-angular, subequal to their intervals, suture to suture, evanescing on last whorl in parietal region, most prominent at periphery of body whorl; early whorls with 13 ribs, decreasing to 12 on penultimate whorl, obsolete on last quarter whorl. Spiral lirae on spire whorls thin, angular, prickly where cross axials, upper one situated a short distance below suture, lower one slightly above succeeding suture. Anterior end of body whorl with 14 spiral lirae, those on rostrum raised, subequal, flattening out and becoming more widely set above rostrum, where they appear as paired furrows.

Pale salmon-coloured, sometimes darker on periphery of body whorl, ribs and subsutural region white, salmon-tinged in area above suture.

Protoconch papillose, of slightly fewer than 2 whorls, smooth, apically moderately convex and bearing a conspicuous brown spot; breadth 0.63-0.70 mm.

Operculum oblong-ovate, yellowish-brown.

Dimensions.

10.6 x 4.1 mm (holotype); larger paratype (with juvenile lip) with length 11,2 mm.

Notes.

Immature paratypes of this species show much similarity to *Columbella chuni* Thiele, 1925, based on juvenile material from 404-463 m off Tanzania (THIELE 1925: 142, pl. 19, fig. 6). Comparison with syntypes of *C. chuni* (BMNH 1948.12.10.1-2) shows that *A. blignautae* differs in its non-shouldered whorls, flat-sided, sharper spire and much more elongate base and aperture. From the three Western Atlantic species referred here by RADWIN (1978) it differs in its elongate aperture and more fusiform shape (almost suggestive of the New World genus *Strombina* Mörch, 1852).

Etymology.

Named after Mrs Tracy Blignaut, assistant to Brian Hayes.

Family OLIVIDAE

Genus *Ancillista* Iredale, 1936

KILBURN (1993: 372) regarded *Ancillaria hasta* Martens, 1902, of the Agulhas Bank, as an atypical member of this genus. A second South African species is here added, on the grounds of its large protoconch and non-ridged columella base. Nevertheless it is unique within the Ancillinae in its totally smooth, straight, non-differentiated columellar pillar. When the body is known, this species will probably prove to belong to an undescribed genus. Terminology after KILBURN (1977).

Ancillista depontesi n. sp.

Figs 3-5

Type material.

Holotype NMSA V4381/T1532, off Kenton-on-Sea, 101 m, coarse sand and shell debris, dead, Natal Museum Dredging Programme. Paratypes 1-2, NMSA V6144/T1553, same data as holotype; paratype 3, NMSA V6143/T1551, between Great Fish and Keiskamma River mouths, 100 m, in crayfish trap, with operculum, B. Hayes. Paratypes 4-6 in B. Hayes collection; paratype 4, same data as paratype 3; paratype 5, off Algoa Bay, 100 m, in crayfish trap; paratype 6, off Port Alfred, 100 m, crayfish trap.

Additional (non-type) material.

"Zululand", 100-200 m, crayfish trap, locality doubtful, in B. Hayes collection.

Type locality.

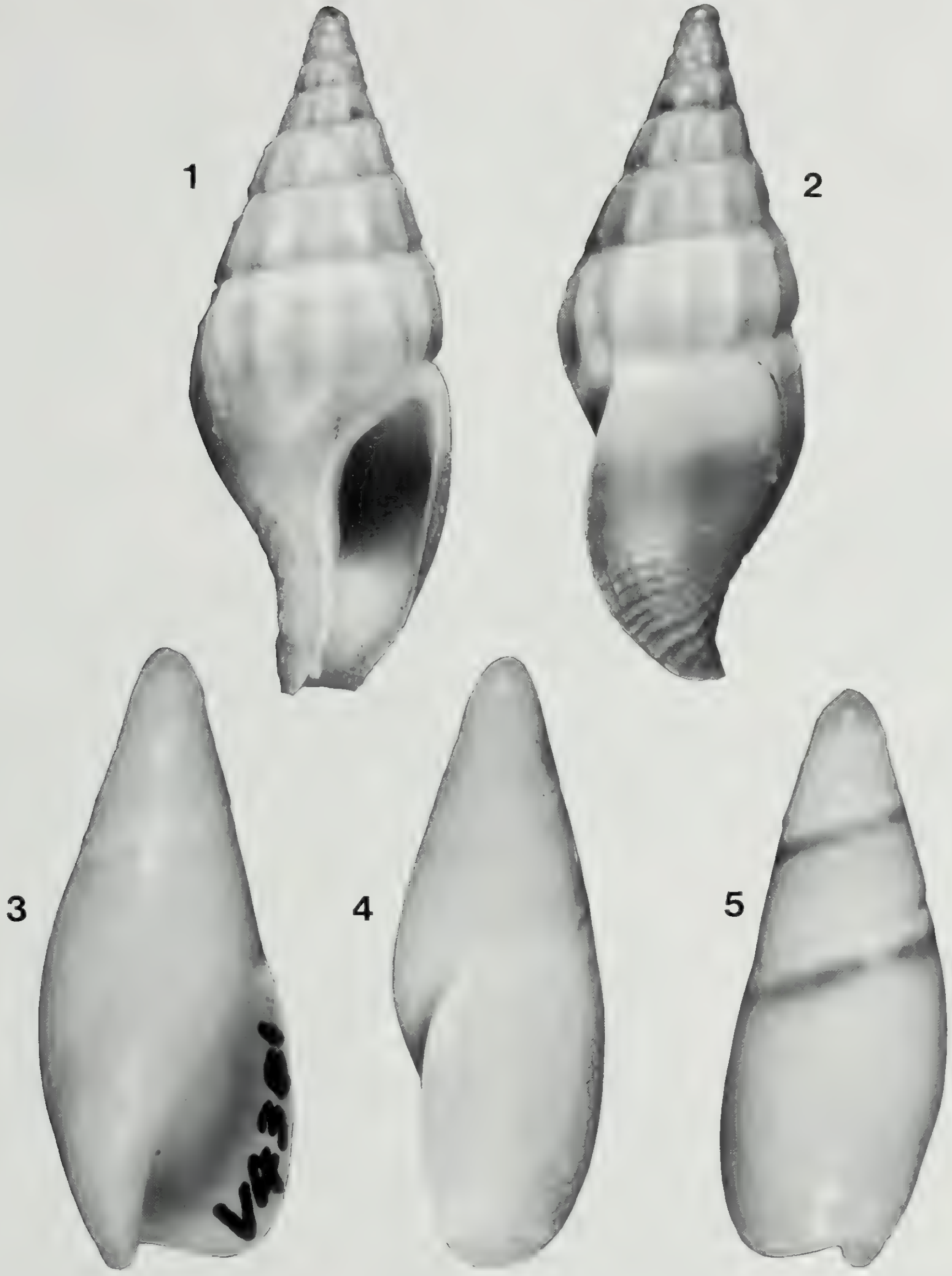
Off Kenton-on-Sea (33°55.6'S; 26°44.0'E), eastern Algoa Bay, 101 m.

Distribution.

Eastern Agulhas Bank, from off Algoa Bay to the Keiskamma/Great Fish River area.

Diagnosis.

Shell cuneiform with bluntly rounded apex, rather flat-sided spire and wide anterior end; base of columella broad and straight, not twisted, nor defined by an anterior fasciolar groove; primary spire callus thin, covering body whorl, slightly indented where covers suture, and forming a low ridge above suture, without distinct microscopic granules, although these are present on the thin secondary callus pad at end of penultimate whorl and on columella; ancillid band almost level, defined by shallow grooves; off-white with a milk-white zone below suture, followed by a narrow light to dark orange-brown band. Maximum length 20.4 mm.



Figs 1-2. *Anachis (Suturoglypta) blignautae* (Columbellidae), n. sp. Holotype NMSA V6140/T1548, off Richard's Bay, Zululand, 600 m, dimensions 10.6 x 4.1 mm. **Figs 3-5.** *Ancillista depontesi* (Olividae), n. sp. Figs 3-4. Holotype NMSA V4381/T1532, off Kenton-on-Sea, E. Algoa Bay, 101 m, dimensions 18.2 x 7.6 mm. Fig. 5. Paratype V6144/T1553, same locality, dimensions 16.3 x 6.3 mm.

Description.

Shell wedge-shaped with blunt apex, rather straight-sided spire and broad anterior end, breadth/length 0.39-0.42; body whorl more convex on left side than on right, greatest width of shell at about 0.30 length from base, aperture/total length 0.44-0.47; apical region slightly cyrtoconoid, protoconch obtuse and rather rounded, spire angle about 30°. Primary spire callus thin, covering body whorl, slightly impressed at suture, which it scarcely masks, protoconch exposed; surface of spire callus glossy, not distinctly microshagreened, lacking spiral sculpture other than a low angular ridge of callus immediately above suture; secondary callus very thin, forming a microshagreened pad at end of penultimate whorl and covering inner lip.

Aperture cuneiform, gaping basally, widest about 0.25 from anterior end, columella slightly foreshortened; outer lip thin, in side view evenly convex, without an ancillid tooth, siphonal notch deeply, broadly and asymmetrically concave. Columella not forming a twisted pillar, broad and straight, with very fine microshagreen sculpture. No anterior fasciolar groove; inner lip very shallowly and evenly concave anteriorly, straight posteriorly. Ancillid band very slightly declivous, almost level, demarcated by a very shallow groove on either side; median zone with rather coarse growth lines. Termination of protoconch not demarcated, total number of whorls about 5.5.

Cream-colour, subsutural margin milk-white, followed by a diffuse light to dark orange-brown stripe.

Operculum transparent pale yellowish, rounded-trigonal with non-terminal, eccentric nucleus, about 0.45 length of aperture.

Dimensions.

18.2 x 7.6 mm (holotype), 20.4 x 8.4 mm (largest paratype).

Notes.

Ancillista depontesi bears little resemblance to any of its congeners, but is superficially most similar to *Bullia ancillaeformis* E. A. Smith, 1906, in the Nassariidae. This resemblance is obviously the result of convergence, as it differs from the latter in possessing an ancillid band. From the other Agulhas Bank species, *Ancillista hasta* (Martens, 1902), it differs *inter alia* in the body whorl being uniformly covered with primary callus and in the presence of an ancillid band and groove.

Etymology.

Named in honour of Captain Zeca de Pontes, who first discovered this unusual species.

Superfamily **CONOIDEA**
Family **DRILLIIDAE**
Genus ***Splendrillia*** Hedley, 1922

The material of this genus then available from southern Africa was revised by KILBURN (1988:206-218), who recorded a total of 8 species. The species described below is referred to *Splendrillia* on account of the restriction of spiral sculpture to the rostrum.

Splendrillia hayesi n. sp.
Figs 6-7

Type material.

Holotype NMSA V6142/T1550; paratype 1, in B. Hayes collection.

Type locality.

Off Algoa Bay, 100 m, in crayfish pots.

Distribution.

Eastern Agulhas Bank, known only from the type locality.

Diagnosis.

Claviform (breadth/length 0.36-0.37, aperture/total length 0.36-0.40), rostrum bent to right, with a strong fasciole and chink-like umbilicus; whorls strongly rounded, upper third concave, flattened below suture; anal sinus deep, asymmetrically U-shaped, constricted by thick parietal pad; moderately glossy, axial ribs low, opisthocline, 9 on body whorl, evanescing below suture and on base at parietal level, no spiral sculpture except numerous, weak threads on rostrum; protoconch large and papillose; uniform white. Maximum length 26.7 mm.

Description.

Shell claviform (breadth/length 0.36-0.37, aperture/total length 0.36-0.40), of 7 teleoconch whorls, with blunt apex, body whorl obconical with moderately short, distinctly oblique, tapering anterior end; suture moderately shallow, not undulating; whorls strongly rounded, more angular on early whorls, periphery just below midwhorl, forming a slight shoulder on last whorl; upper third of each whorl concave, flattening out below suture (without a distinct cord or sulcus); left side of anterior end of body whorl concave, with a strong fasciole (bending rostrum to left) and chink-like false umbilicus. Aperture oblong-pyriform, greatest width at about posterior third, siphonal canal moderately deep and wide, rather

Figs 6-7. *Splendrillia hayesi* (Drilliidae), n. sp. Holotype NMSA V6142/T1550, off Algoa Bay, 100 m, dimensions 22.7 x 8.2 mm. **Figs 8-9.** *Turris faleiroi* (Turridae), n. sp. Holotype NMSA V6145/T1554, off Algoa Bay, 100 m, dimensions 40.4 x 12.3 mm.

straight, termination not dorsally indented. Inner lip almost straight, with thick callus, edge concave in parietal region where callus forms a thick posterior pad, constricting anal sinus. Outer lip chipped in all types but strongly convex in side view, with deep, rather asymmetrically U-shaped anal sinus, stromboid notch evidently very slight.

Surface moderately glossy; sculptured by low axial ribs only, except for numerous, weak spiral threads on rostrum; no definite prelabral varix, growth lines coarse. Axial ribs opisthocline, in transverse section angularly rounded, more or less equal to intervals, 9 on 1st whorl, 10-12 on penultimate whorl, becoming obsolete on last 0,2 of body whorl; ribs obsolete below suture and at parietal level, appearing as smooth, oblong nodules on body whorl. Uniform white.

Protoconch large and papillose but too worn or encrusted for details.

Dimensions.

22.7 x 8.2 mm (holotype), 26.7 x 10.3 mm (paratype).

Notes.

Of its known South African congeners, only the much narrower, salmon-coloured *Splendrillia daviesi* Kilburn, 1988, approaches *S. hayesi* in size. Of Indo-Pacific taxa the most similar is probably *S. solicitata* (Sowerby, 1913) of the Western Pacific, which has distinctly shouldered axial ribs and faint colour zones. *S. hayesi* is superficially similar to another Agulhas Bank species, *Agladrillia ukuminxa* Kilburn, 1988, but that is much smaller, with spiral threads overall and a straight rostrum.

Family **TURRIDAE**

Genus ***Turris*** Röding, 1798

The southern African species of this genus were revised by Kilburn (1983: 552). Much further material has subsequently been acquired during the Natal Museum Dredging Programme and will be dealt with in a future paper. However, the present species is particularly noteworthy in being the first temperate-water member of the genus known.

Turris faleiroi n. sp.

Figs 8-9

Type material.

Holotype NMSA V6145/T1554; paratype 1, NMSA V6146/T1555, juvenile; paratypes 2-3 in B. Hayes collection; all from type locality, in crayfish pots.

Type locality.

Off Algoa Bay, 100 m.

Distribution.

Eastern Agulhas Bank, known only from the type locality.

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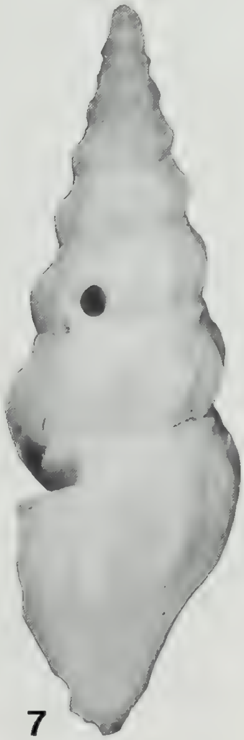

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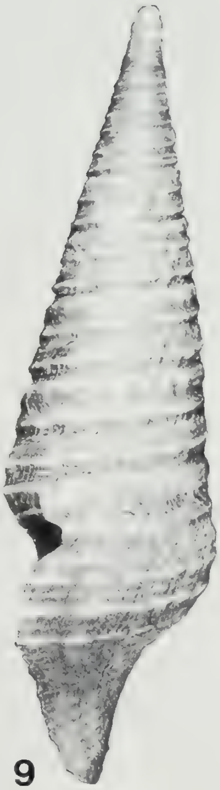

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Diagnosis.

Medium-sized, fusiform with aperture/total length 0.34-0.36, spire orthoconoid, whorls moderately flat, shoulder sulcus shallow, subsutural cord broad, with 3-4 spiral lirae, shoulder cord moderately thin, weakly crenulate, periphery of base with 3 strong cords and weak intermediaries; collabral threads sharp and crispate, rendering most spiral lirae pliculate; anal sinus shallow; protoconch large (breadth 1.60-1.75 mm); reddish-brown, spiral lirae paler, flecked below suture and elsewhere with pale reddish-brown. Maximum length 43.5 mm.

Description.

Shell with 11 teleoconch whorls, breadth/length 0.30-0.31), aperture short (aperture/spire 0.34-0.36), spire orthoconoid with flattened whorls and shallow suture; subsutural cord low, rather ill-defined, bearing 3-4 spiral lirae and microscopic spiral threads, crenulated or pliculated by axial sculpture; shoulder sulcus shallow. Anal sinus shallow, asymmetrical; shoulder (sinus) cord as strong as other cords, weakly and irregularly crenulated. Periphery of base with 3 well-defined, subequal main cords, each pair separated by 1 intermediary lira flanked by several weaker threads; 2 of these cords are visible on spire whorls (making a total of 4 cords per whorl), although the lower may be hidden in suture; 1st teleoconch whorl already with 4 thin lirae, the lower two closer together. Anterior end of body whorl with 20-25 lirae, those on rostrum close and even, those above stronger and more wide-set, their intervals with fine spiral threads. Fine, sharp, crispate collabral threads overall, crenulating all main lirae.

Light brown with paler main lirae, bearing an occasional slightly darker reddish-brown fleck, protoconch light brown. Traces of dull light brown periostracum retained interstitially.

Protoconch papillose, large and blunt, of about 1.8 whorls, last 0.6 whorls with 8-16 strong, arcuate axial ribs, with a spiral lira developing a short distance above suture near termination; breadth 1.60-1.75 mm.

Dimensions.

40.4 x 12.3 mm (holotype), 43.5 x 12.2 mm (largest paratype, lip damaged).

Notes.

Turris faleiroi is very similar to another South African endemic, *Turris orthopleura* Kilburn, 1983, which lives somewhat further east on the continental shelf of Transkei and southern Natal. It differs from *T. orthopleura* in its larger protoconch (breadth 1.60-1.75 mm against 1.30-1.50 mm), which is less papillose but has a more inflated first whorl; the suture in *T. faleiroi* is much deeper, axial threads are much stronger and sharper, rendering the spirals somewhat crenulate, the subsutural cord bears 3 distinct spiral lirae, instead of only fine threads, spiral cords are slightly stronger, the shoulder sulcus is deeper and the ground colour pale brown instead of white.

Etymology.

Named after Mr Ginger Faleiro, captain of the crayfish boat that first discovered this species.

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A simple shell model: applications and implications

Bernard TURSCH

Laboratoire de Bio-Écologie, Faculté des Sciences,
Université Libre de Bruxelles, 50 av. F.D. Roosevelt, 1050 Brussels, Belgium.

KEY WORDS. Gastropods, shell, model.

ABSTRACT. A simple computer-assisted, non-mathematical procedure for emulating sagittal sections of Gastropod shells is described. Examples illustrate that the final "shell" shapes can largely be predicted from the values of the construction parameters. The problem of the meaning of traditional descriptions of the shape of shells is briefly addressed.

1. INTRODUCTION

Coiled shells are the hallmark of most living Molluscs and all Brachiopods, amounting to about half of all non-arthropod invertebrates. They also constitute a large proportion of all fossils. The fascination long exerted on biologists, mathematicians and other artists by the regular shapes of shells is reflected in a copious literature and an abundant iconography. As it could be expected, many mathematical models have been proposed to explain or imitate the growth of coiled shells. Most of these models have been reviewed by MEINHARDT (1995) and STONE (1996). For many years, the standard tool for the geometrical analysis of coiled shells has been the model developed by the eminent palaeontologist D.M. Raup in a series of papers culminating in his well-known 1966 synthesis.

A simple, operational model of coiled shells has been recently developed (TURSCH, 1997a). The model was intended as a probe for biological studies rather than for realistic simulation of specialised structures, so it could be kept very easy. It has several advantages over other shell models. Amongst others, it rests upon independent parameters and can simulate shells with non-isometric growth (for instance Gastropods with concave or convex spires) without having to postulate *ad hoc* changes in the shell parameters (which amounts to make constants vary). The basic shape of the shell (this does not account for spines, sculpture, etc.) is entirely determined by the construction parameters.

One short paragraph in the original paper stated that the outcomes of the construction are largely predictable by comparing the values of the parameters. Detailed examples will now be given.

Some conchologists have been made insensitive to the joys of mathematics. Yet they can easily produce rough simulations of sagittal shell sections without using any equation at all, by using a small computer equipped with one of the many drawing programs now in common use. The step by step procedure (very summarily outlined in TURSCH, 1997a) will be described here. It is particularly suited for simulating the shells of multi-coiled Gastropods.

A computer program that automatically generates "shells" can easily be derived from the model. If one aims at the mass production of shell models, the use of such a program will save several minutes on every construction. If one aims at understanding the role of the individual parameters and appreciating how these parameters do interact, then the step by step, hands-on procedure is certainly more informative.

Understanding shell parameters can be of importance for evaluating the descriptions of the shape of shells, which are at the very foundations of mollusc taxonomy. Let us consider the two shells depicted in Fig. 1. The obvious difference in their aspect would ordinarily be described by listing differences in the states of a series of traditional shell characters. These may be the general outline of the shell, the height of the spire, the shape and orientation of the aperture, the convexity of the whorls, etc. In works of taxonomy, the question of whether the characters in this list are independent of each other or are not is very rarely raised, if ever. It might be instructive to see how these different traditional characters relate to differences in shell parameters.

This paper is about shapes and relies heavily on illustrations. For the study of shapes, one drawing speaks better than a thousand words, a bunch of equations or a few pages of computer program listing.

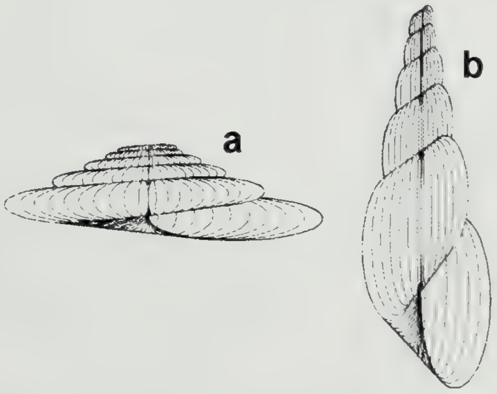


Figure 1. The problem of shell description. How do these two shells differ? (see text § 1).

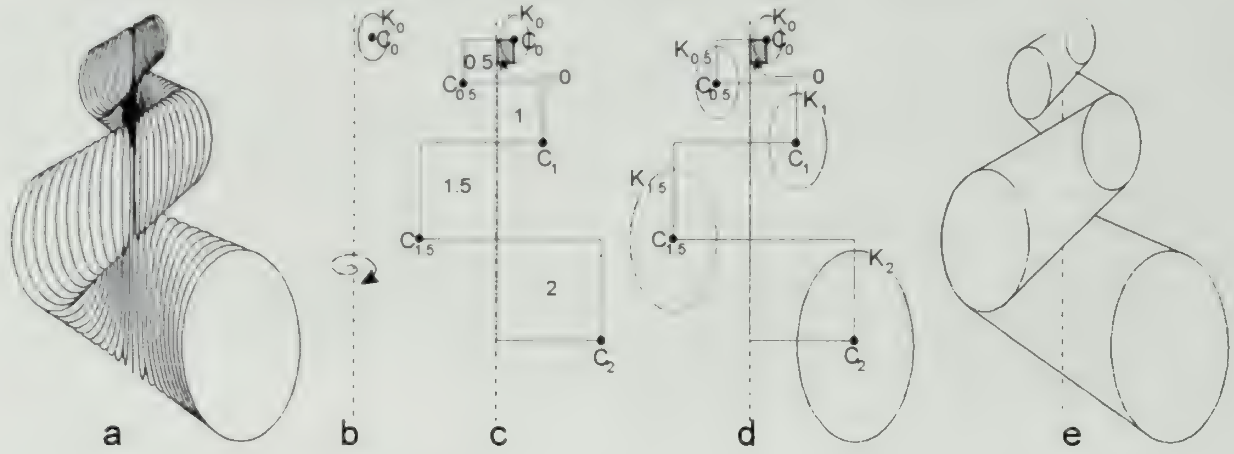


Figure 2. The shell model: general principle (see text § 2.1).

2. THE MODEL

2.1. Generalities

As in most other shell models, the "shell" is the surface of revolution produced by a regularly growing generating curve (the shell aperture) effecting a helicospiral motion along an axis (the coiling axis). The generating curve K_0 is, as usual, taken to be an ellipse because the aperture of most shells can be approximated by (or inscribed in) this shape.

To simulate the sagittal section of a shell (such as the shell in Fig. 2, a) one first has to position in relation to a coiling axis a starting ellipse K_0 of suitable shape and size (Fig. 2, b).

One then determines where the centre of the generating curve K_0 will be located at each subsequent half-volution (Fig. 2, c). C_0 is the centre at the start and $C_{0.5}$, C_1, $C_{1.5}$, C_2, ..., C_n are the centres after 0.5, 1, 1.5, 2, ..., *n* revolutions. The position of these successive centres are found by building the successive rectangles "*0.5*", "*1*", "*1.5*", etc. They are all simply derived (by the use of appropriate parameters) from an essential element in the starting configuration: rectangle "*0*" (darkened in Fig. 2, c and d). Obtaining rectangle "*0*" will be explained in detail in § 3.1.1.

The starting figure K_0 is then "grown" by an appropriate factor to obtain $K_{0.5}$, K_1, $K_{1.5}$, K_2, etc., each of which is the placed on its calculated centre $C_{0.5}$, C_1, $C_{1.5}$, C_2 (Fig. 2, d).

If so desired, sutures can be drawn and the aspect of the whorls can be simulated by joining the edges of $K_{0.5}$, K_1, $K_{1.5}$, K_2, etc. with appropriate lines (Fig. 2, e).

The suitably positioned ellipse K_0, the three points C_0, C_1, C_2 and three growth parameters do completely determine all the construction, no matter the number of whorls.

2.2. Parameters

The parameters of the model have been defined in TURSCH (1997a). This has to be repeated here, to make the construction procedure comprehensible.

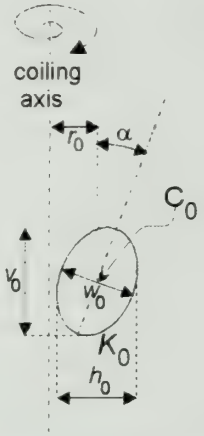


Figure 3. Parameters for shaping and positioning the generating curve K_0 (see text § 2.2.2).

2.2.1. Parameters determining the starting conditions

The size and proportions of the starting ellipse K_0 (see Fig. 3) are determined by its smallest diameter $\boldsymbol{w_0}$ (here always equal to 1) and its ellipticity $\boldsymbol{e}$ (the ratio of its longer axis to the shorter).

The spatial orientation of the ellipse K_0 in relation with the coiling axis is described in the complete model (see TURSCH, 1997a) by three angular parameters α, β and δ. In the simplified, rough simulation presented here, the generating ellipse K_0 is always *co-planar with the axis*, so parameters β and δ will be neglected. Parameter α is the angle of the long axis of K_0 with the coiling axis.

Parameter ***q*** is defined as:

$$q = r_0 / (h_0/2) \quad \text{so} \quad r_0 = q.(h_0/2)$$

Particular case: if angle $\alpha = 0$ then

$$h_0 = w_0 \quad \text{and} \quad r_0 = q.(w_0/2)$$

If angle $\alpha = 0$ and if K_0 is tangent to the coiling axis (a common case) then $r_0 = (w_0/2)$ and $q = 1$.

2.2.2. Parameters positioning the centre after one volution

Positioning the centre C_1 amounts to determining d_0 and r_1 (see Fig. 4). Parameter ***p*** has been defined as

$$p = d_0 / (v_0/2) \quad \text{so:} \quad d_0 = p.(v_0/2)$$

Particular case: if angle $\alpha = 0$ then

$$v_0 = e.w_0 \quad \text{and} \quad d_0 = p.(ew_0/2)$$

Parameter $\mathcal{R}$ (the rate of ***R***adial expansion) has been defined as

$$\mathcal{R} = r_1 / r_0 \quad \text{so} \quad r_1 = \mathcal{R}.r_0$$

Parameter $\mathcal{R}$ applies to all subsequent whorls, so

$$\mathcal{R} = r_1 / r_0 = r_n / r_{n-1} \qquad \textbf{(1)}$$

2.2.3. Parameters positioning the centre after two volutions

Positioning point C_2 (see Fig. 4) amounts to determining d_1 and r_2.

Parameter $\mathcal{L}$ (the rate of ***L***ongitudinal expansion) has been defined as

$$\mathcal{L} = d_1 / d_0 \quad \text{so} \quad d_1 = \mathcal{L}.d_0$$

This parameter applies to all subsequent whorls, so

$$\mathcal{L} = d_1 / d_0 = d_n / d_{n-1} \qquad \textbf{(2)}$$

r_2 depends on parameter $\mathcal{R}$ defined here above:

$$r_2 = \mathcal{R}.r_1$$

2.2.4. Growth of the generating curve

This amounts to determining w_1, the diameter after one revolution.

The growth of the generating curve after one volution determines parameter $\mathcal{W}$ (the rate of ***W***horl expansion)

$$\mathcal{W} = w_1 / w_0$$

One will notice that $\mathcal{W}$ is the same as Raup's parameter *W*. This parameter applies to all subsequent whorls, so

$$\mathcal{W} = w_1 / w_0 = w_n / w_{n-1} \qquad \textbf{(3)}$$

2.2.5. Subsequent volutions

Each subsequent centre C_n is placed in relation to the preceding centre C_{n-1} by direct application of parameters $\mathcal{R}$ and $\mathcal{L}$ [see expressions (1) and (2)]. The size of each subsequent motive K_n is simply that of the previous motive K_{n-1} multiplied by parameter $\mathcal{W}$ [see expression (3)].

2.2.6. Remarks

The internal definition of $\mathcal{L}$ (the only originality in this otherwise obvious model) allows one to dodge the problem of having to select a point of origin for the helico-spiral. The position of this point in relation to K_0 determines much of the shape of the resulting surface of revolution, a difficulty that has plagued previous models.

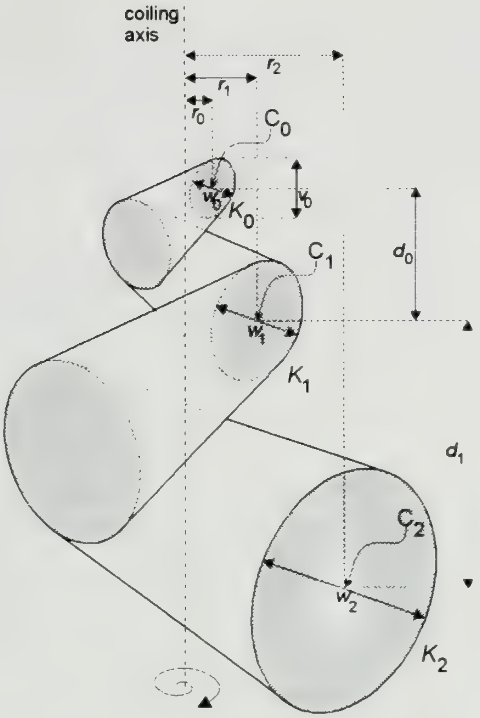


Figure 4. Construction: parameters for developing shell whorls (see text § 2.2.1).

The parameters of the model are of two very distinct kinds (see TURSCH 1997a). Parameters *q*, *p*, *e*, and α are fixed ***initial conditions***, and it is tempting to speculate that they reflect an embryonic *répertoire* (see TURSCH 1997a). Parameter *p* only sets the pitch of the first volution. Parameter *q* is defined from an initial distance r_0 and is useful for model construction and analysis convenience. In contrast, parameters $\mathcal{W}$, $\mathcal{R}$ and $\mathcal{L}$ are ***expansion rates***. They just selectively amplify the starting parameters during growth, as long as *n* (the number of volutions) has not reached its final value.

3. APPLICATIONS

Drawing program requirements. The program should be able to draw lines, rectangles, ellipses and circles. It should also be able to group, move, rotate, mirror and scale objects (by stretching vertically and horizontally) by a given percentage. Most of the recent drawing programs allow these operations.

Graphic conventions. The step by step graphic constructions are made mostly by stretching and moving selected elements. In each step, the copy of a starting element (thick lines, light shading) is stretched horizontally by *x*% and vertically by *y*% (indicated by **H**= *x*%; **V**= *y*%). It is then moved as indicated by arrows to yield a resulting element (very thick lines, dark shading). This is often the starting element for the next step. For typographic facility, square roots are indicated in the text as: $p^{0.5}$.

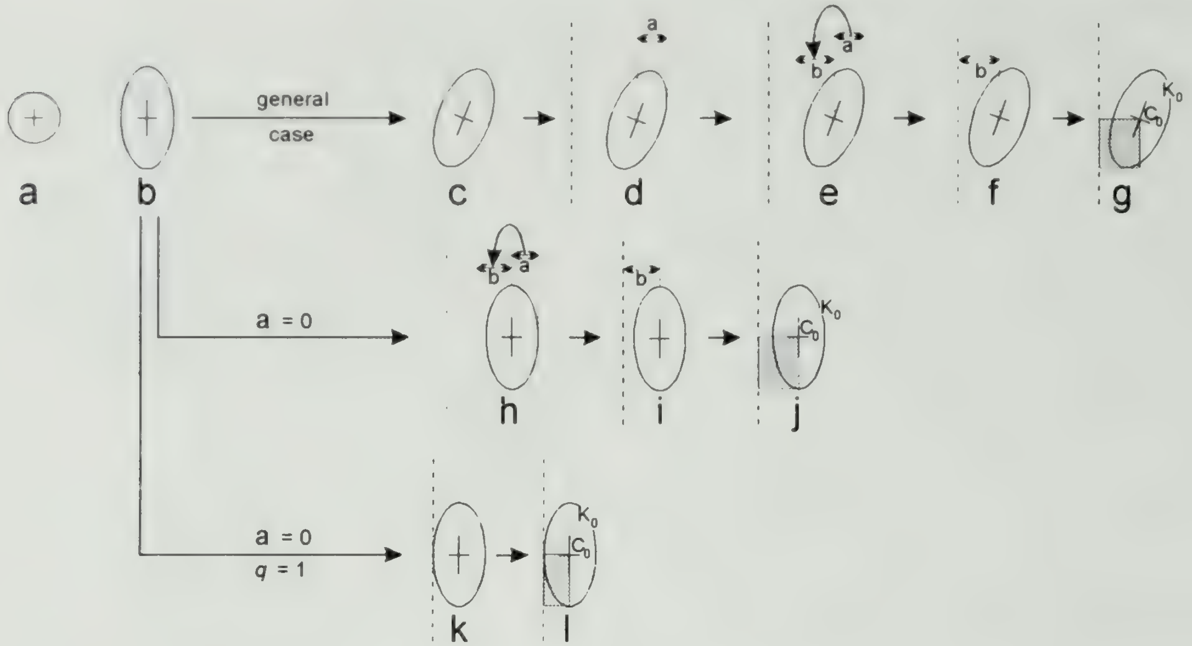


Figure 5. Construction: generating and placing the starting elements (see text § 3.1).

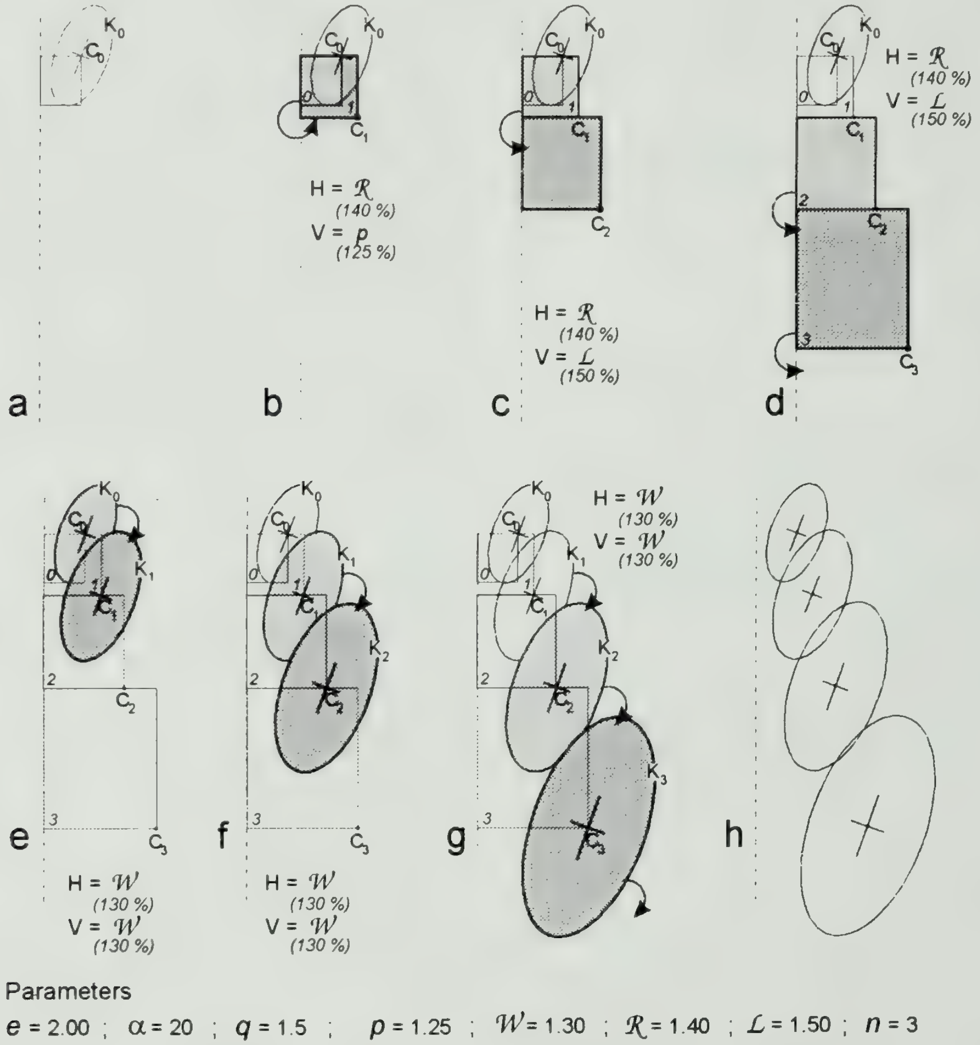


Figure 6. Construction of sagittal half sections (see text § 3.2).

3.1. Construction: starting elements

All constructions require the same first steps: the positioning of the starting ellipse K_0 and the construction of rectangle "*0*".

3.1.1. Starting ellipse

Parameters needed: *e*, *q* and α. Let us take as example: $e = 2$; $q = 1.5$; $\alpha = 20$.

a. Draw two crossed lines (see Fig. 5, a). From their intersection as a centre, draw a circle of diameter w_0 (this has necessarily an ellipticity $e = 1$). With the command "*group*" (or similar) associate the lines with the circle into one single picture (the position of the centre will be needed to allow accurate positioning during the remainder of the construction). w_0 will be the length unit.

b. This figure is now stretched vertically by 200 % (in order to obtain an ellipse with the desired ellipticity $e = 2$) (see Fig. 5, b).

c. Rotate the ellipse by an angle α (in this case 20°) (see Fig. 5, c).

d. Draw the coiling axis and any line perpendicular to the axis (see Fig. 5, d). Build segment a.

e. Stretch horizontally a copy of segment a by 150 % (because $q = 1.5$) to obtain segment b, which is then placed as shown (see Fig. 5, e).

f. Position the ellipse at a distance b from the coiling axis (see Fig. 5, f). The generating curve K_0 is now fully positioned, with its centre C_0 marked by intersecting lines.

g. Erase all unnecessary features. Draw rectangle "*0*" (see Fig. 5, g). This will be the stepping stone for the remainder of the construction.

3.1.2. Particular cases

a. The construction is simplified if $\alpha = 0$ (ellipse parallel to the axis). Segment **a** (see Fig. 5, h) is now the half diameter $w_0/2$ of the ellipse. The next two steps (see Fig. 5, i and j) are straightforward.

b. Things are especially simple if $\alpha = 0$ and $q = 1$ (a very common case). All one has to do is then to bring directly the ellipse tangent to the axis (see Fig. 5, k) and draw rectangle "*0*" (see Fig. 5, l).

c. One will note that if $e = 1$ then α is indeterminate (rotating a circle by any amount yields the same circle).

TIPS: Make the starting ellipse small enough because it might grow very much (your computer program can "*zoom*" on small features). Most shells can be simulated by placing the starting ellipse tangent to (or very close to) the axis.

3.2. Construction: sagittal half sections

These constructions are very fast and extremely simple because no calculation at all is needed. Sagittal half-sections most often contain enough information to grasp the final shape of the whole "shell". All parameters are set in advance. The recipe is illustrated step by step in Fig. 6.

3.2.1. Starting elements

The starting elements (Fig. 6, a) are obtained as described in § 3.1, illustrated in Fig. 5. In this example: $e = 2$; $q = 1.5$; $\alpha = 20$.

3.2.2. Centre after first volution.

Parameters needed: $\mathcal{R}$ and *p*. In this example $\mathcal{R} = 1.4$, $p = 1.25$.

The position of centre C_1 (Fig. 6, b) is found by stretching a copy of rectangle "*1*" horizontally by 140% (because $\mathcal{R} = 1.40$) and vertically by 125% (because $p = 1.25$).

3.2.3. Centre after second volution.

Parameters needed: $\mathcal{R}$ and $\mathcal{L}$. In this example: $\mathcal{R} = 1.40$, $\mathcal{L} = 1.5$.

The position of centre C_2 (Fig. 6, c) is found by stretching a copy of rectangle "*1*" horizontally by 140% (because $\mathcal{R} = 1.40$) and vertically by 150% (because $\mathcal{L} = 1.5$). This new rectangle (rectangle "*2*") is placed as shown in Fig. 6, c. The remainder of the positioning of the subsequent centres is now repetitive.

3.2.4. Centres of subsequent volutions

Parameters needed: $\mathcal{R}$ and $\mathcal{L}$, as above.

The position of centre C_3 (Fig. 6, d) is found by stretching a copy of rectangle "2" horizontally by 140% (because $\mathcal{R} = 1.40$) and vertically by 150% (because $\mathcal{L} = 1.5$). This new rectangle (rectangle "3") is then placed as shown. For a "shell" with n volutions, the same procedure is repeated until one obtains rectangle "n", determining the position of centre C_n.

3.2.5. Generating curve after one volution

Parameter needed: $\mathcal{W}$. In this example: $\mathcal{W} = 1.30$.

Figure K_1 is obtained (see Fig. 6, e) by stretching a copy of the starting ellipse K_0 horizontally and vertically by 130% (because $\mathcal{W} = 1.30$). This new figure is then placed with its centre (marked with intersecting lines) exactly at point C_1. The "growth" and the positioning of the generating curve at the subsequent volutions are now repetitive

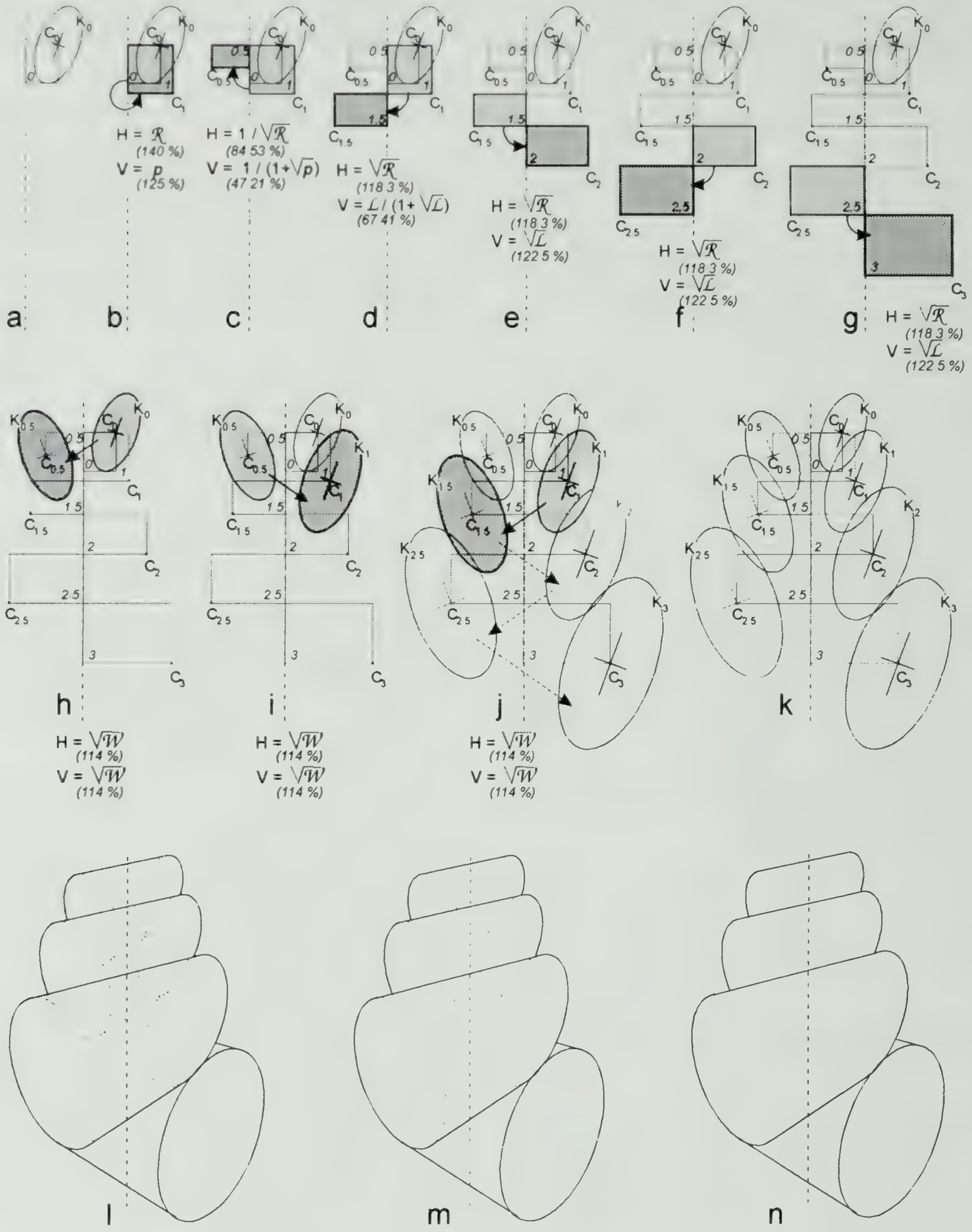
3.2.6. Generating curve at subsequent volutions

Parameter needed: $\mathcal{W}$, as above.

Figure K_2 is obtained (see Fig. 6, f) by stretching a copy of the starting ellipse K_1 horizontally and vertically by 130% (because $\mathcal{W} = 1.30$). This new figure is then placed with its centre (marked with intersecting lines) exactly at point C_2. The "growth" and the positioning of the generating curve at the subsequent volutions is now repetitive (see Fig. 6, g). For a "shell" with *n* volutions, the same procedure is repeated until one obtains ellipse K_n, centred on C_n.

3.3. Construction: sagittal full sections

All parameters are set in advance. The procedure now entails the construction of the "shell" at each half-volution. Two steps do require simple transformations of the parameters.



Parameters: $e = 2.00$; $\alpha = 20$; $q = 1.5$; $p = 1.25$; $\mathcal{W} = 1.30$. $\mathcal{R} = 1.40$; $\mathcal{L} = 1.50$; $n = 3$

Derived values: $1/(1+\sqrt{p}) = 0.4721$; $\sqrt{\mathcal{W}} = 1.140$; $\sqrt{\mathcal{R}} = 1.183$; $1/\sqrt{\mathcal{R}} = 0.8453$; $\sqrt{\mathcal{L}} = 0.6441$; $\mathcal{L}/(1+\sqrt{\mathcal{L}}) = 0.6441$

Figure 7. Construction of sagittal full sections (see text § 3.3).

3.3.1. Starting elements

As for sagittal half-sections (§ 3.2), the starting elements (Fig. 7, a) are obtained as described in § 3.1 and illustrated in Fig. 5. In this example: $e = 2$; $q = 1.5$; $\alpha = 20$.

3.3.2. Centre after first volution

This step is the same as for sagittal half-sections (see § 3.2.2).

Parameters needed: $\mathcal{R}$ and p. In this example $\mathcal{R} = 1.4$, $p = 1.25$.

The position of centre C_1 (Fig. 7, b) is found by stretching a copy of rectangle "*1*" horizontally by 140% (because $\mathcal{R} = 1.40$) and vertically by 125% (because $p = 1.25$).

3.3.3. Centre after 0.5 volution

Parameters needed: $\mathcal{R}$ and p. One has to calculate the values of $\mathcal{R}^{0.5}$ (here: 1.183) and $1/(1+ p^{0.5})$ (here: 0.4721).

The position of centre $C_{0.5}$ is found by stretching a copy of rectangle "*0*" horizontally by 118.3% (because $\mathcal{R}^{0.5} = 1.183$) and vertically by 47.21% [because $1/(1+ p^{0.5}) = 0.4721$]. This new rectangle (rectangle "*0.5*") is placed as shown in Fig. 7, c.

3.3.4. Centre after 1.5 volution

Parameters needed: $\mathcal{R}$ and $\mathcal{L}$. One has to use $\mathcal{R}^{0.5}$ (in this example: 1.183) and $\mathcal{L}/(1+\mathcal{L}^{0.5})$ (here: 0.6741).

The position of centre $C_{1.5}$ is found by stretching a copy of rectangle "*1*" horizontally by 118.3% (because $\mathcal{R}^{0.5} = 1.183$) and vertically by 47.21% [because $\mathcal{L}/(1+ \mathcal{L}^{0.5}) = 0.4721$]. This new rectangle (rectangle "*1.5*") is placed as shown in Fig. 7, d.

3.3.5. Centre after two volutions

Parameters needed: $\mathcal{R}$ and $\mathcal{L}$. One has to use $\mathcal{R}^{0.5}$ (in this example: 1.183) and $\mathcal{L}^{0.5}$) (here: 1.225).

The position of centre C_2 is found by stretching a copy of rectangle "*1.5*" horizontally by 118.3% (because $\mathcal{R}^{0.5} = 1.183$) and vertically by 122.5% (because $\mathcal{L}^{0.5}= 1.225$). This new rectangle (rectangle "*2*") is placed as shown in Fig. 7, e.

3.3.6. Centres of subsequent volutions

Parameters needed: $\mathcal{R}^{0.5}$ and $\mathcal{L}^{0.5}$, as above.

The position of centre $C_{2.5}$ (Fig. 7, f) is found by stretching a copy of rectangle "*2*" horizontally by 118.3% (because $\mathcal{R}^{0.5} = 1.183$) and vertically by 122.5% (because $\mathcal{L}^{0.5}= 1.225$). This new rectangle (rectangle "*2.5*") is placed as shown. For a "shell" with n volutions, the same procedure is repeated until one obtains rectangle "*n*", determining the position of centre C_n (see Fig. 7, g).

3.3.7. Generating curve after 0.5 volution

Parameter needed: $\mathcal{W}^{0.5}$. In this example: $\mathcal{W} = 1.30$ and $\mathcal{W}^{0.5}= 1.14$.

Figure $K_{0.5}$ is obtained (see Fig. 7, h) by rotating a copy of the starting ellipse K_0 by an angle $-\alpha$, then stretching it horizontally and vertically by 114% (because $\mathcal{W}^{0.5} = 1.14$). This new figure is then placed with its centre (marked with intersecting lines) exactly at point $C_{0.5}$. The "growth" and the positioning of the generating curve at the subsequent volutions are now repetitive.

3.3.8. Generating curve at subsequent volutions

Parameter needed: $\mathcal{W}^{0.5}$, as above.

Figure K_1 is obtained (see Fig. 7, i) by "rotating a copy of the ellipse $K_{0.5}$ by an angle $-\alpha$, then stretching it horizontally and vertically by 114% (because $\mathcal{W}^{0.5} = 1.14$). This new figure is then placed with its centre (marked with intersecting lines) exactly at point C_1. The "growth" and the positioning of the generating curve at the subsequent volutions is now repetitive (see Fig. 7, j). For a "shell" with n volutions, the same procedure is repeated until one obtains ellipse K_n, centred on C_n.

The procedure might look more difficult than it really is. With a little practice, once the derived values have been established, steps a to k (in Fig. 7) are easily effected in less than 5 minutes.

3.3.9. Final image

The final image (Fig. 7, k) can now be made up by masking hidden parts, drawing sutures and delineating the shape of whorls (for instance as in Fig. 7, l, m or n). Whorl resorption occurs in many Gastropods. According to the desired type of model, one can elect to have the "aperture" mask the previous whorl or not.

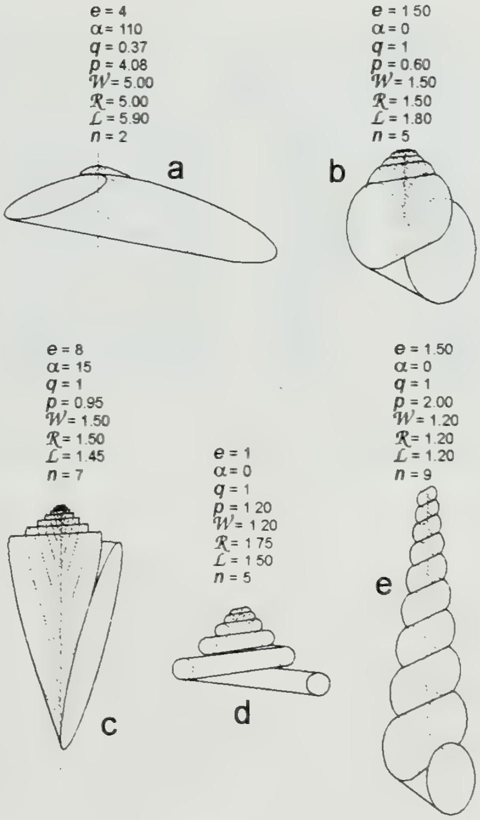


Figure 8. Construction: examples of applications (see text § 3.3.9).

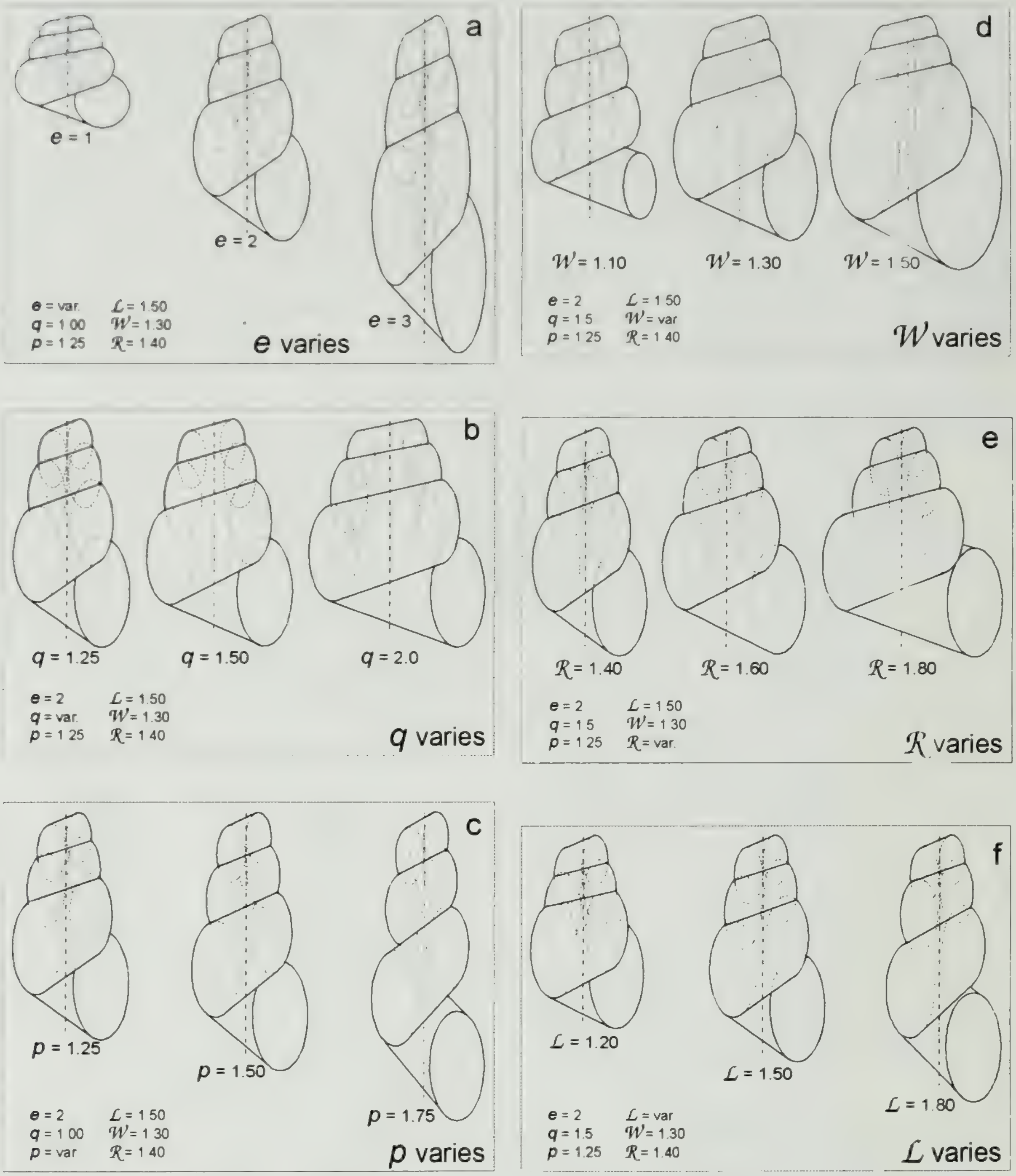


Figure 9. Shape variations due to changes in a single parameter (see text § 4.1).

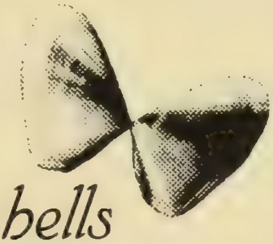
Rather realistic renditions of many existing shells are easily produced by the graphic construction described here above (see Fig. 8, illustrating a few familiar cases). For even more realism, the shape of the starting ellipse could be modified, for instance by adding or substracting suitable features. With so many variables, it would take a very long time to produce a given "shell" by experimenting with arbitrary combinations of parameters. The task is very much simplified if one understands how each individual parameter acts and how given combinations of parameters do affect the final shape.

4. THE CONTROL OF SHAPE

Easy "rules of construction" can be deduced from the model. Some are given here under as examples. Many more could be found by an interested reader.

4.1. Effect of individual parameters

Examples of the changes resulting from the variation of individual parameters are shown in Fig. 9. The effect of the expansion parameters $\mathcal{W}$, $\mathcal{R}$ and $\mathcal{L}$ are quite predictable. One will notice that the final shape is extremely dependent from the initial conditions q, p and e.



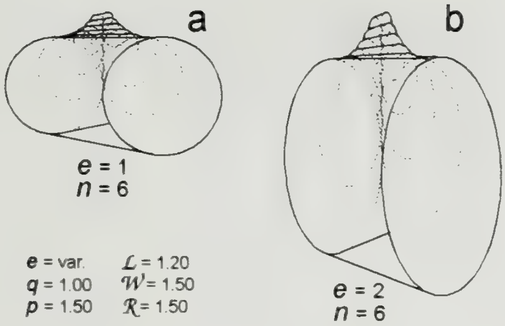


Figure10. Parameter ***e*** affects not only the shape of the body whorl but also the shape of the spire (see text § 4.1).

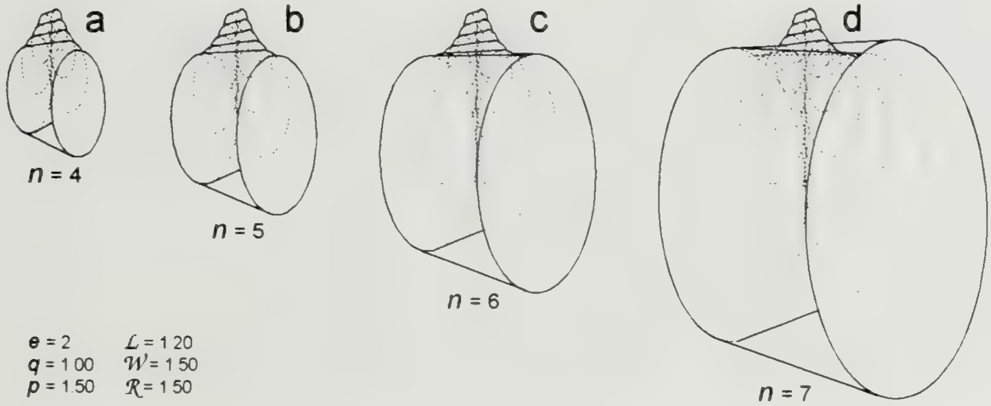


Figure 11. Non-isometric growth without change in shell parameters. The shape of the shell varies with the number of whorls *n*. (see text § 4.1).

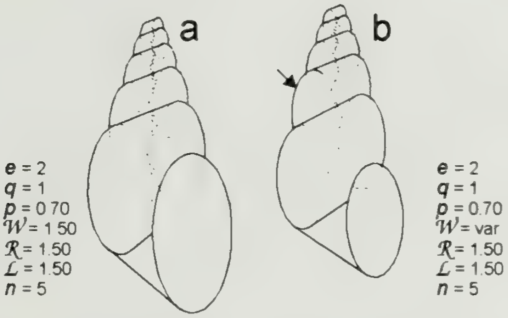


Figure 12. Non-isometric growth by abrupt change of a shell parameter. The construction of shell **a** yields shell **b** if at whorl 2.5 (marked by an arrow) one changes the value of *W* from 1.5 to 1.2 (see text § 4.1).

Fig. 10 shows that *e* (the ellipticity of the generating curve) influences not only the shape of the body whorl but also the shape of the spire. Some more dramatic effects of parameter *e* will be shown in § 4.3.

The shape of many shells (most shells, according to VERMEIJ 1993) does vary during growth. In contrast to others, this model can produce "shells" with non-isometric growth (see Fig. 11) without having to modify progressively the values of parameters. It is thus quite important to specify a value for *n* (the number of whorls).

Abrupt changes in the value of parameters do happen during the growth of some real shells (for an example, see TURSCH 1997b). This can of course be easily emulated in this step by step procedure by modifying any of the expansion parameters $\mathcal{W}$, $\mathcal{R}$, or $\mathcal{L}$ at any desired point of the construction (for an example, see Fig. 12).

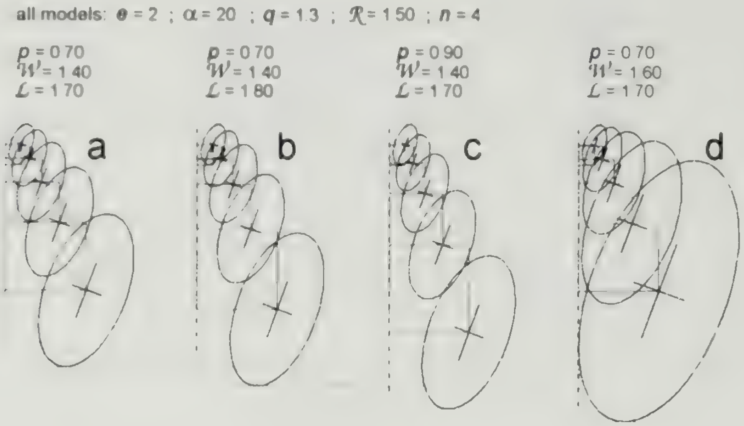


Figure 13. General features of the shell are affected by individual variations of several parameters. For instance, all other parameters kept constant, the length of a given shell (a) is modified by a change of L (b), of p (c) or W (d). (see text § 4.2).

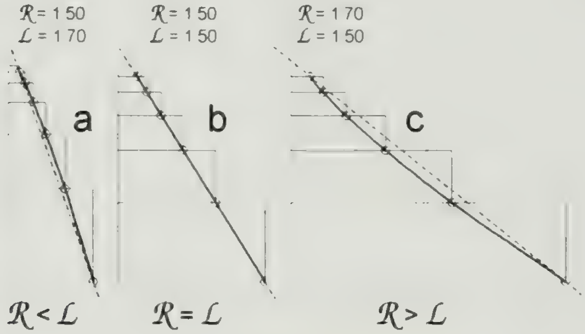


Figure 14. The relation of R to L determines the alignment of the centres (see text § 4.2.1).

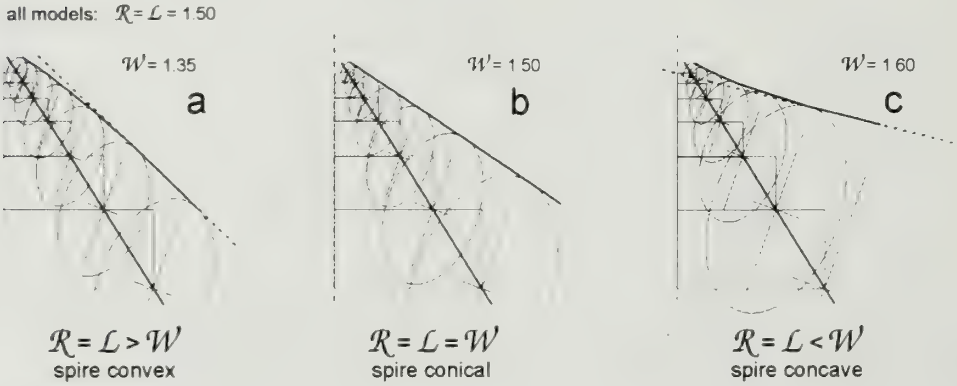


Figure 15. If $R = L$ then the value of W determines the shape of the spire (see text § 4.2.2).

General features of the shell are affected by individual variations of several parameters. For instance, the total length depends on both the rate at which the centre of the aperture moves "down" the coiling axis (the compounded effects of p and $\mathcal{L}$) *and* the growth rate of the aperture ($\mathcal{W}$). Therefore, all other parameters being the same, individual variations of p, of $\mathcal{W}$ or $\mathcal{L}$ will affect the total length of the "shell" (see Fig. 13). In the same way, the diameter (at any moment of growth) depends on both the growth rate of the aperture ($\mathcal{W}$) *and* the rate at which the centre of the aperture moves away from the coiling axis ($\mathcal{R}$).

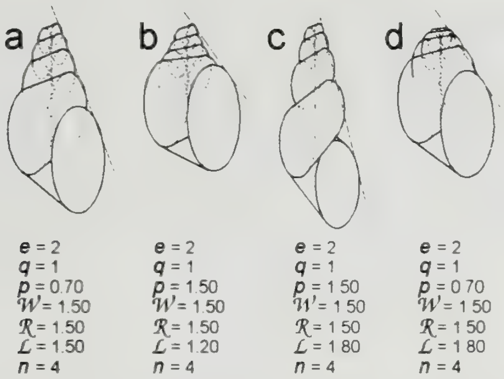


Figure 16. If q = 1 and *W* = *R* then all the whorls are tangent to the coiling axis (see text § 4.2.2).

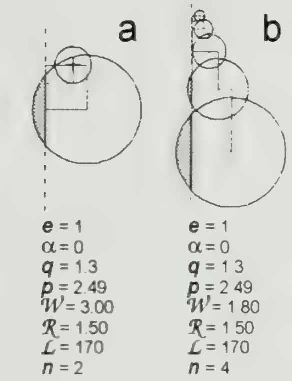


Figure 17. If *W* > *R* then fabricational problems may occur (see text § 4.2.2).

4.2. Effect of combinations of parameters

By their definition, all the parameters are completely independent from each other (this was not the case of the parameters in the classical model of RAUP 1966). However, the shape of the final "shell" depends very much on the interaction of these independent parameters.

4.2.1. Parameters $\mathcal{R}$, $\mathcal{L}$ and $\mathcal{W}$

If $\mathcal{R} = \mathcal{L}$ then, in sagittal view, all the centres are aligned on a straight line. The revolution of the centre of the generating curve takes place on a conical surface (see Fig. 14, b). If $\mathcal{R} < \mathcal{L}$ the surface of revolution of the centres will be convex (see Fig. 14, a); if $\mathcal{R} > \mathcal{L}$ it will be concave. (see Fig. 14, c). Note: these relations determine only the positions of the centres, not the outline of the shell.

If $\mathcal{R} = \mathcal{L} = \mathcal{W}$ then growth will be isometric, leading to shells with true conical spires (see Fig. 15, b). If $\mathcal{R} = \mathcal{W} \neq \mathcal{L}$ then growth will be non-isometric, the shape of the shell varying during growth (see § 4.1). If $\mathcal{R} = \mathcal{L} > \mathcal{W}$ the spire will be convex (Fig. 15, a). If $\mathcal{R} = \mathcal{L} < \mathcal{W}$ the spire will be concave (Fig. 15, c).

4.2.2. *Parameter q*

If $q = 1$ then the generating curve K_0 is tangent to the coiling axis (see the definition of q).

If $q = 1$ and $\mathcal{W} = \mathcal{R}$ then all the whorls are tangent to the coiling axis, whatever the values of the other parameters. This is a very common case in real Gastropods, as illustrated by the few examples in Fig. 16.

If $q = 1$ and $\mathcal{W} = \mathcal{R} = \mathcal{L}$ then all the whorls are tangent to the coiling axis and the shell is conispiral (Fig. 16, a).

If $\mathcal{W} > \mathcal{R}$ and if the number of volutions is not limited, the whorls will ineluctably increase beyond the coiling axis. If $q = 1$, this overlap will occur right at the start of the construction. If $q > 1$ it may happen either at the start (Fig. 17, a) or after a few volutions (Fig. 17, b), depending on the values of the other parameters. This does not necessarily constitute an insurmountable fabricational constraint. In real shells, the problem may be solved in various ways, for instance by the resorption of previous whorls or by changes in the angular parameter β (not treated here, but see TURSCH 1997a).

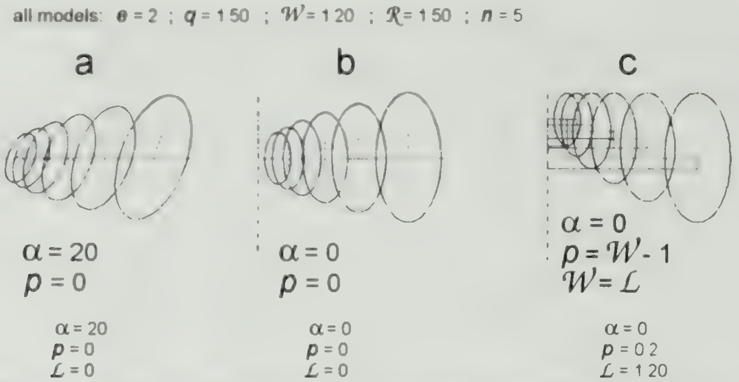


Figure 18. The construction of isostrophic and discoidal "shells" (see text § 4.2.3).

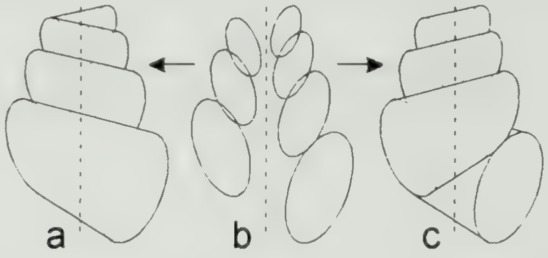
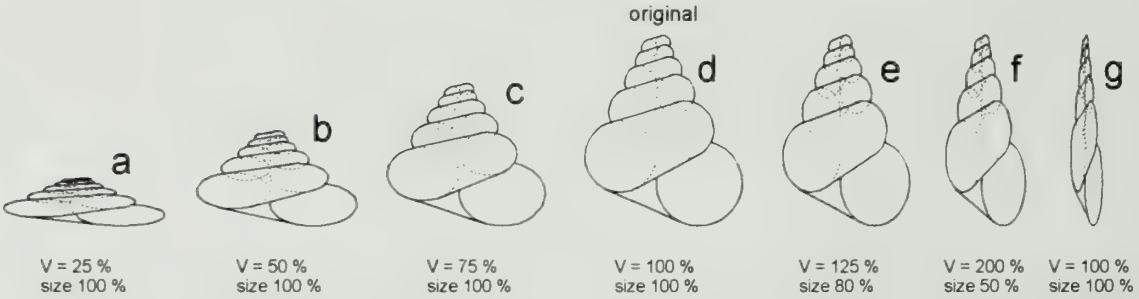
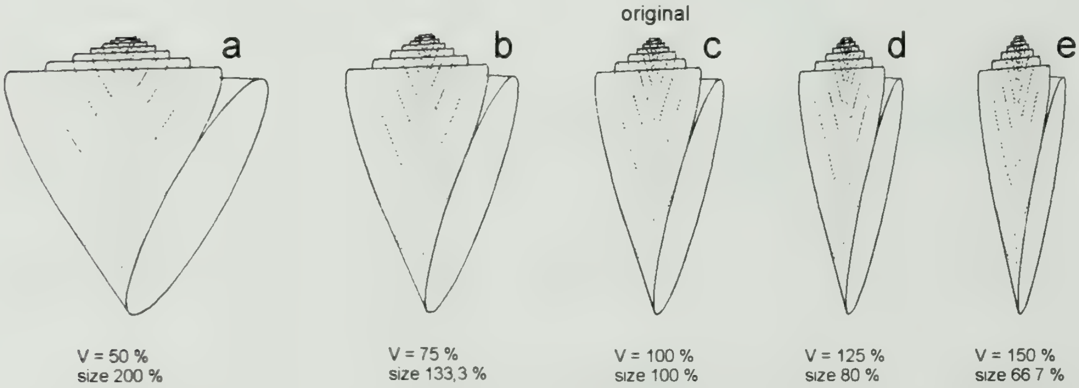


Figure 19. Dextral end sinistral shells (see text § 4.2.4).



Original image: $e = 1.50$; $\alpha = 0$; $q = 1$; $p = 1.50$; $\mathcal{W} = 1.20$; $\mathcal{R} = 1.20$; $\mathcal{L} = 1.20$; $n = 5$

Figure 20. The stretching of whole images. The case $\alpha = 0$ (see text § 4.3).



Original image: $e = 8.00$; $\alpha = 15$; $q = 1$; $p = 0.95$; $\mathcal{W} = 1.50$; $\mathcal{R} = 1.50$; $\mathcal{L} = 1.45$; $n = 7$

Figure 21. The stretching of whole images. The case $\alpha \neq 0$ (see text § 4.3).

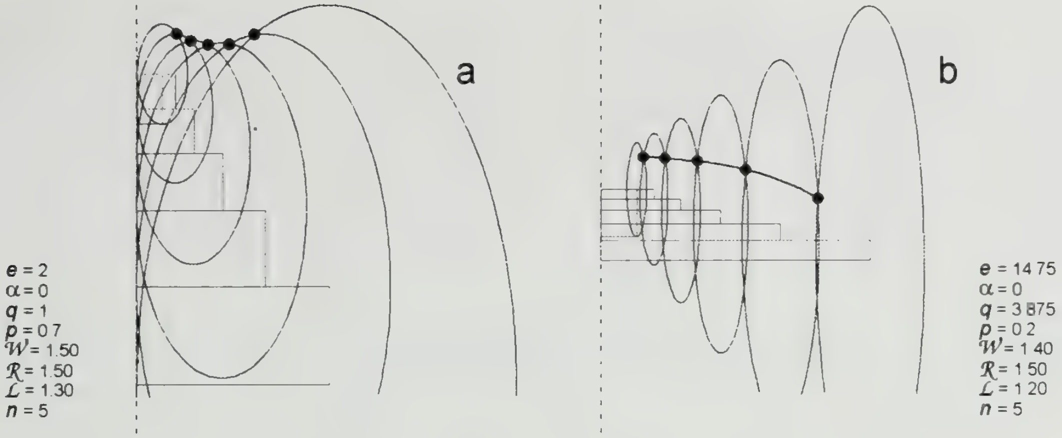


Figure 22. The problems of the suture (see text § 5.1).

4.2.3. Parameter *p*

If $p = 0$ then $\mathcal{L}$ is indeterminate (its value is irrelevant for the construction). All the centres are located in the same plane, perpendicular to the coiling axis (Fig. 18, a).

If $p = 0$ and $\alpha = 0$ then the "shell" is *isostrophic* (has a plane of symmetry) (Fig. 18, b). Note that the word "planispiral" has been avoided here, as it can be taken in different meanings (see COX 1955, ARNOLD 1965).

$p = \mathcal{W} - 1$ and $\mathcal{W} = \mathcal{L}$ and $\alpha = 0$ is the condition for the "shell" to be *discoidal* (Fig. 18, c).

4.2.4. Dextral and sinistral "shells"

The observant reader will have noticed that the model does not specify the direction of coiling. Both dextral and sinistral "shells" can be obtained from the same construction (see Fig. 19). Sinistral shells (of entirely different nature) can be obtained by assigning negative values to parameter *p* or to parameter $\mathcal{L}$. Note: one has then to take the negative square root of the absolute value.

4.3. Modification of completed models

Once a model has been completed, it is easy to modify its shape by stretching the whole image (all parts having been linked into one single image by using the command "group"). This generates very rapidly "shells" of various shapes. But what is one then really doing?

If $\alpha = 0$ in the original image, then vertical or horizontal stretching modifies only parameter *e*. An example of related images obtained by vertical stretching is given in Fig. 20. The magnitude of the observed changes in shape fully confirms the conclusions of § 4.1. Stretching "shells" does of course change their sizes. Many will have to be reduced or enlarged accordingly, to allow better comparison of shapes.

If $\alpha \neq 0$ in the original image, then vertical or horizontal stretching does modify the value of both parameters e and α, as shown in Fig. 21.

5. IMPLICATIONS

5.1. Suture

The suture has been often used in shell morphometry because it is mostly easy to observe and lends itself well to a variety of measurements. However, the suture is a feature of much more complex nature than conchologists generally assume.

The suture is the locus of the outermost points belonging to two consecutive whorls. Determining the equation of the suture in terms of shell parameters is far from being elementary. Conversely, attempting to deduce the shell parameters from the suture would be extremely difficult (if possible at all).

Careful examination of sutures can nevertheless give most useful information. Abrupt changes in the aspect of the suture often indicate abrupt changes in parameters (for an example, see TURSCH 1997b: 98).

The example depicted in Fig. 22, a shows that the suture does not necessarily describe a regular helicospiral: it starts by going "down" then goes "up" (this condition, although uncommon, is met in some real shells with a sunken spire, such as *Oliva concavospira* Sowerby, 1914). The revolution surface on which the suture is inscribed is also not easily deduced from the surface of revolution of the centres or even from the profile of the spire. This can be seen on the example of Fig. 22, b. In this sagittal section, the suture goes "down" the axis while the spire goes "up".

Small differences in shell parameters can produce large differences in the aspect of the suture and more work is definitely needed to clarify the properties of this familiar shell feature.

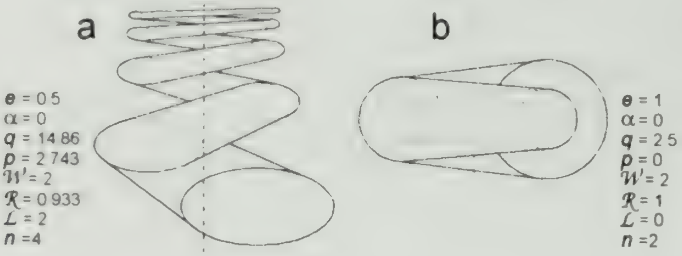


Figure 23. Two examples of "impossible shells" (see text § 5.2).

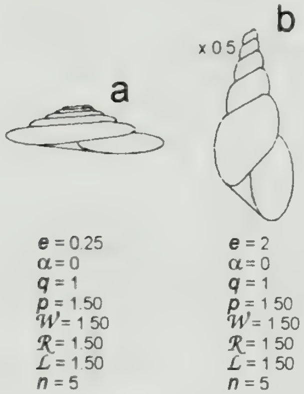


Figure 24. Shell parameters *vs.* traditional characters of shape. Variation of one single parameter (see text § 5.3).

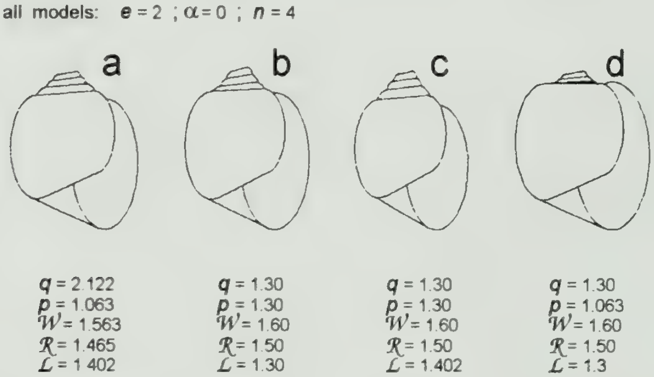


Figure 25. Shell parameters *vs.* traditional characters of shape. Variation of several parameters (see text § 5.3).

5.2. "Impossible shells"

Besides imitating known shells, the model can also produce "shells" that we can not (not yet? not anymore?) have in our collections. Many strange shapes are possible and only two examples will be given here. Some of these constructions meet obvious fabricational problems (for instance the "shell" in Fig. 23, b), some others seem perfectly feasible (see Fig. 23, a).

Accumulating a collection of such "impossible shells" is amusing but is not only a game. It constitutes an excellent tool for finding and maybe explaining the "forbidden avenues" of evolution in the "shell morphospace" (this is the set of all possible outcomes from a given geometrical/mathematical model). The interest of this classic problem in evolutionary biology has been recently emphasised by DAWKINS (1996).

5.3. Shell parameters *vs.* traditional characters of shape

The basic shape of shells (and of their parts) is usually described by a series of traditional characters (general outline of the shell, height of the spire, shape and orientation of the aperture, convexity of the whorls, etc.). The correlation between shell parameters and the conventional shell descriptions raises a number of questions.

Example A. "Shells" **a** and **f** in Fig. 20 are exactly the same as the shells depicted in Fig. 1. On the one hand, these shells have a completely different aspect, reflected by large differences in many traditional characters of shape. On the other hand, the two shells are very closely related in terms of shell parameters. They differ only by parameter *e*, as can be seen in Fig. 24 where all their parameters of the two shells are now given.

Example B. Conventional descriptions of the two closely matching "shells" **a** and **b** in Fig. 25 would be extremely similar, yet these two "shells" differ by the values of no less than five parameters. The smallness of the variation of each parameter does not justify the observed similarity. Let us modify shell **b** by changing only parameter $\mathcal{L}$ by the same amount. One then obtains shell **c**, of noticeably different shape (see Fig. 25). Modifying only parameter q leads to shell **d**, of quite different aspect. The similarity is due to another cause: the effects of the variations in individual parameters nearly cancel each other. In real shells, this would be a nice case of convergence (possibly a case of sibling species).

Example A raises an immediate question. Do the different traditional shell characters really represent distinct characters? Example B shows that the traditional descriptors of basic shape do not necessarily reflect differences in shell parameters.

Example A shows that the conventional characters of shape are certainly correlated. All are entirely determined by the parameters of the model. All can change simultaneously by modifying one single parameter. Traditional descriptors of basic shape only *appear* to be independent. This illusion is simply due to the reductionistic way by which we describe a complex structure. We proceed by dividing it in arbitrary, smaller parts then describing these parts in succession.

The shell parameters being completely independent, one could be tempted to consider that each of them is a shell character. This would raise a serious problem. Indeed, we would then be compelled to consider that the very different shells **a** and **b** are more closely related than the very similar shells **b** and **c**. Fortunately, this does not happen. Shell parameters do not satisfy the conditions required for characters measuring phyletic similarity. They cannot be absent (thus precluding evolutionary novelty); there are no "primitive" and no "derived" parameters.

The very fact that we can (most often) recognise species by their shells establishes that the shell parameters, albeit mathematically independent, are *biologically* correlated. So there is no "description vs. parameters" paradox if one considers that it is the *whole set* of shell parameters that constitutes one single, numerical shell character. This holistic approach of shells reminds of the notion of "*morphological integration*" of Nemeschkal (1991).

It is the very same shell character that conventional descriptions attempt to convey (this time with words instead of figures). If the growth of the shell is regular (with constant parameters) then the whole set of the many traditional shell "characters" describing the basic shape of the shell and of its parts constitutes one single character.

It is not suggested that the whole set of shell parameters is controlled by one single gene! Most probably, these parameters do not even exist in nature as separate entities. They are parts of a model that *describes* the growth, not of natural law that *causes* a particular type of growth.

5.4. Deriving parameters from real shells

This paper concerns the building of conceptual "shells" from a set of predetermined parameters. What does it imply about the reverse operation: deriving parameters from real shells?

In the simple case of regular growth, the minimum requirements for finding all the parameters are: the correct positioning of the coiling axis, the determination of the co-ordinates of the centres at least at 3 accurately determined positions, the determination of the increase of the generating surface between at least at 3 accurately determined positions.

These very simple requirements are fraught with problems because small experimental errors in measurements may lead to serious discrepancies. A reliable, accurate method for exact positioning of the axis has yet to be published. Determination of the position of the centres is anything but evident, especially if the generating curve is not a true ellipse (it rarely is). Further problems arise because, in contrast to real shells, the theoretical shell model is an immaterial surface, without any thickness. One should also note that the same difficulties will be met with all other helico-spiral shell models.

Similar shells may differ by a number of parameters (see § 5.3.B), so really accurate determination of their values seems *a priori* quite difficult. To estimate shell parameters, graphic simulations are possibly more operational than shell measurements.

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A new species of *Zebina* (Gastropoda: Rissoidae: Rissoininae) from Yucatán (Mexico)

E. ROLÁN

Cánovas del Castillo 22, 36202 Vigo, Spain

KEYWORDS. Rissoininae, *Zebina*, new species, Yucatan, Mexico.

ABSTRACT. *Zebina unamae* n. sp. is described. The species was found in Yucatan, Mexico, Caribbean Sea. It is compared with related species.

INTRODUCTION

The subfamily Rissoininae is represented by numerous species in the Caribbean. They have been treated in general books, such as CLENCH & TURNER (1950), WARMKE & ABBOTT (1961), ABBOTT (1974), VOKES & VOKES (1983), LEAL (1991), DÍAZ MERLANO & PUYANA HEGEDUS (1994), and in revisions such as that of DESJARDIN (1949), or in comparison with the species of other areas, as in SLEURS (1989, 1993). The nearby fauna of Brasil is mentioned in SOUZA LOPEZ *et al.* (1966) and in RIOS (1985).

Numerous species have already been described in this subfamily. Nevertheless, some new ones have been recently added (see DE JONG & COOMANS, 1988; FABER, 1990).

In 1994 the author was in Mexico, invited to participate in the "Primera Reunión de Vinculación Académica sobre Tópicos Malacológicos". Some sediment samples were collected snorkeling in front of the Puerto Morelos Station of the Institute for Marine Sciences and Limnology of the National Autonomous University of Mexico (UNAM). Two shells from this sediment were sufficiently different from any known Caribbean species to be considered as new to science, and are the subject of the present work.

Genus *Zebina* H. & A. Adams, 1854

Zebina unamae n. sp.
(Figs. 1-4)

Type material.

Holotype (Fig. 1), 1.54 x 0.94 mm, deposited in the Museo Nacional de Ciencias Naturales of Madrid, (n° 15.05/31010), and one paratype (Fig. 2), 1.87 x 0.91 mm, in the collection of the author.

Type locality.

Puerto Morelos, Estación of the UNAM, 15 km west of Cancún, Quintana Roo, Yucatán, Mexico.

Etymology.

The specific name is dedicated to the UNAM, the institution which invited us to a scientific meeting and from which Station we collected the sediment samples in which the shells were found.

Description.

Shell (Figs. 1-2) oval-elongate with rissoiniform features, apex acute, with the last whorl representing more than half of the total shell length.

Protoconch (Fig. 3) conical and smooth, of non-planktotrophic larval type, with 1½ whorls.

Teleoconch with about three to four whorls increasing rapidly in size. The spiral sculpture is the most important, consisting of very prominent cords. These cords number five on the first whorl of the teleoconch, decreasing to three on the second whorl; an additional cord appears on the third whorl from the suture below; on the last whorl there are 8-10 prominent spiral cords, with those of the base being smaller.

Microsculpture (Fig. 4): the spiral cords are strong but irregularly constructed, with many small holes and lateral prolongations. Between the cords, the surface is formed by small deep axial sulci that are irregularly arranged, sometimes crossing and fusing to each other.

Semicircular aperture with an expanded outer lip and deep anal sinus. Columellar lip enlarged, weakly concave. Outer lip enlarged externally, and being a little undulant by the end of the spiral cords. Peristome with one undulating thread and some parallel lines on its inner surface.

Periostracum fine, translucent and adherent.

Discussion.

We have had some doubts about the generic assignment of *Z. unamae* n. sp. It seemed that this species showed more indications of belonging to the genus *Stosicia*, type species *Rissoa planaxoides* Grateloup, 1838, due to its smooth conical protoconch, strong spiral sculpture and axial microsculpture; the external aspect of *Z. unamae* is even rather similar to *Stosicia annulata* (Dunker, 1859), figured in SLEURS (1996). The most important features separating *Z. unamae* from the genus *Stosicia* are the absence of a broad, deep anterior channel (PONDER, 1985) and the lack of a more or less prominent angulation at the inner end of the anterior channel (mentioned in SLEURS, 1996); instead having a deep posterior channel, which is shallow in *Stosicia*. Furthermore, the shell of *Z. unamae* has very weak, parallel threads on the inner side of the outer lip of the aperture, typical of the genera *Zebina* or *Schwartziella*. But in *Schwartziella* the shell always has axial ribs and spiral microsculpture (very different from the sculpture of the present shell), and species of the genus *Zebina* usually have smooth, often shining shells, only sometimes with spiral sculpture (PONDER, 1985). In this situation more importance was attached to the apertural features, rather than to other characteristics, when the final decision was made to assign the present species to the genus *Zebina*.

In view of the difficulty of that decision, we prefer not to suggest an appropriate subgenus based solely on the shell characters.

No other species of the Caribbean region has the spiral sculpture and microsculpture of *Z. unamae* n. sp. The only species with some similarity is *Rissoina hummelincki* De Jong & Coomans, 1988, but that species has axial ribs on the first whorls of the teleoconch and the spiral sculpture is formed by smaller, very numerous cords.

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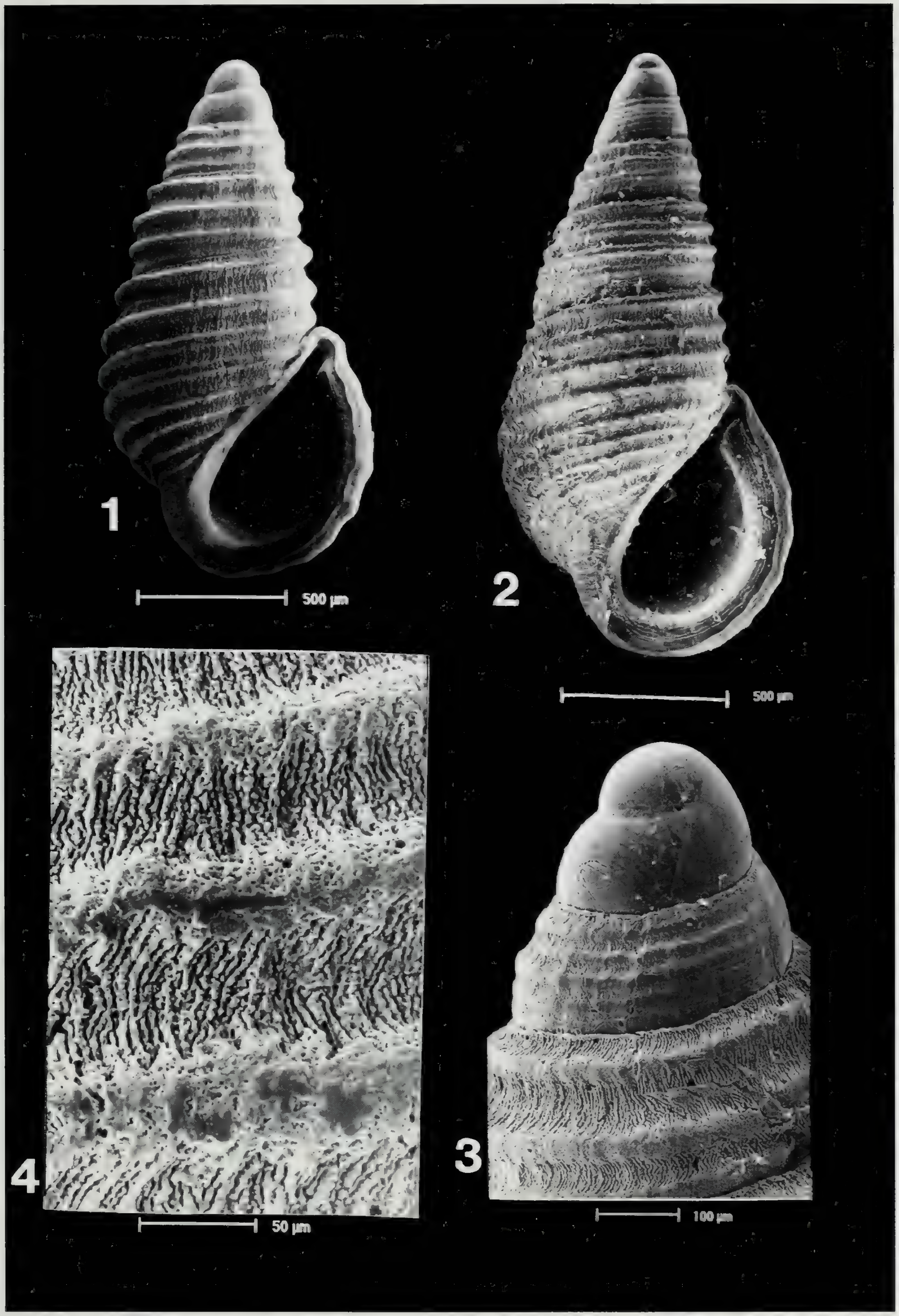

Figs. 1-4. *Zebina unamae* n. sp. Fig. 1. Holotype, MNCN. Fig. 2. Paratype, coll. E. Rolán. Fig. 3. Protoconch of the holotype. Fig. 4. Microsculpture.

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